The accumulation of novel Anthropocene insect communities on native and non-native plants

Roberto Padovani

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University of York

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Abstract

Human-mediated ecosystem alteration and the creation of novel habitats are defining features of the Anthropocene. Understanding more about the ecological and evolutionary 'rules' that govern the accumulation of native species in novel habitats is essential for conservation, whilst determining how non-native species associate with novel habitats is vital to prevent the spread of harmful invasive species across the globe. I propose that non-native plants introduced to Great Britain represent analogues of novel anthropogenic habitats for insects and mites. Non-native plants are an ideal model system as they are widespread, important ecologically, and it is possible to capture their distinctiveness (degree of novelty) effectively with a single quantifiable metric (phylogenetic isolation). I demonstrate that non-native plants typically host less rich and abundant insect communities, although richness and abundance are increased on plants with large geographic ranges, an increased time since introduction, and/or phylogenetic proximity to native plants. Non-native insects are strongly associated with non-native plants, particularly those that are phylogenetically distinctive, which may facilitate the spread of harmful invasive species. Importantly, some non-native plants have the potential to support native insects, as they are associated with similar or even higher levels of insect biodiversity than native plants, and host rare native insect species in the absence of their original native hosts. Thus, mixed plant communities (composed of both native and non-native plants) accumulate insect diversity at similar, or even increased, rates compared with native-only communities. This suggests that non-native plants may contribute to, and potentially maintain, broader-scale (assemblage) diversity in regions that contain mixtures of native and non-native plants. Overall, my work indicates that non-native plants/novel habitats have a real potential to support native biodiversity in an increasingly modified world, although we must be cautious of ecosystem disservices, such as the spread of invasive species and the loss of pre-existing habitats.

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Authors Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

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The two databases associated with this chapter will be publicly available for download once published.

The draft manuscript is reproduced in full in my thesis, with minor formatting alterations. The text was written by myself with input from the co-authors. I carried out all of the data cleaning and processing detailed in the manuscript. A.S. provided access to the RHS database, and advised on its cleaning. W.L. was the original compiler of the DBIF database. M.P. was responsible for preliminary cleaning of the DBIF database. C.D.T. advised on RHS and DBIF data cleaning and processing. D.B.R. provided access to the DBIF database, and advised on its cleaning.

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This manuscript is reproduced in full in my thesis, with minor formatting alterations. The text was written by myself with input from the co-authors. I carried out Vortis suction sampling and insect identification, and designed and carried out analyses. A.S. carried out pollinator sampling and contributed to experimental plot design. H.B. contributed to experimental plot design and oversaw plot maintenance. D.B.R. advised on geographic scale DBIF analysis. C.D.T. advised on overall design, sampling, analysis, and interpretation.

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Chapter 1 General Introduction

A natural heathland habitat

A novel Anthropocene urban green roof habitat

1.1 The Anthropocene: Differing trends in local, regional, and global-scale biodiversity

The Anthropocene is the proposed epoch in recent geological history during which mankind has been a major influence on climate, ecology, and the environment (Waters et al. 2016). Although the Anthropocene is not yet an officially recognised geological epoch, a formal start date of 1950 is likely to be ratified soon (Castree 2016). The proposed date is based upon the deposition of large amounts of radioactive nucleotides and other compounds as a result of large scale nuclear weapons testing in the 1950s, leaving a permanent stratigraphic signature that will probably be observable millions of years into the future (Lewis & Maslin 2015). The main issue with the proposed start date and any alternatives is that they are by definition rooted in geology. Whilst it is true that mankind's influence on the natural world has increased considerably since 1950 (Steffen et al. 2015), we have been altering the world around us for almost as long as we have existed. This began with the Megafauna Extinction (55K years ago - present day), and possibly much earlier (Faurby et al. 2020), and has been characterised by major events such as the Agricultural Revolution (~11,000 years ago), and the Colombian Exchange (1492-1800) (Lewis & Maslin 2015). These events and others have had far reaching consequences for the earth's biotic and abiotic systems.

The creation of novel ecosystems has been one of the defining characteristics of mankind's relationship with the natural world. Novel ecosystems are created directly by processes such as the land conversion of existing environments and the transport of species far beyond their historical dispersal capabilities, and indirectly by various processes such as nutrient run-off from agricultural systems (Hobbs et al. 2009). Categorisation of anthropogenic abiotic and biotic novelty in ecosystems reveals that large areas of the planet are now highly novel compared with historical baselines (Radeloff 2015). The creation of novel ecosystems, such as agroecosystems and cities, provides new habitat niches that are highly divergent from those of pre-existing ecosystems. These novel habitats can help facilitate the establishment of non-native species in new regions without necessarily competing with or displacing native species (providing that some pre-existing ecosystems survive), although large-scale land use change may lead to local native species declines (Thomas 2013a). This is leading to a paradox in modern ecology. Depending on

the scale of biodiversity that is examined different pictures of the direction and magnitude of biodiversity trends emerge. Globally, populations of vertebrate, invertebrate, and plant species, both terrestrial and aquatic, have declined compared with both historical and recent (20th century) baselines (Sax & Gaines 2003; Loh et al. 2005; Dornelas 2014; Newbold 2015). Current species extinction rates are estimated to be considerably higher than historical background rates (Barnosky 2011; Pimm 2014), meaning that global biodiversity declines are likely to continue. Declining biodiversity on a global scale is clearly an issue, and one that should be tackled with appropriate conservation efforts, and by policy, behavioural and cultural shifts. However, to obtain a more complete picture, biodiversity trends must also be examined at the regional and local scale (Thomas 2013a).

Despite global decreases, biodiversity at local and/or regional scales is generally stationary or even increasing (Sax & Gaines 2003; Vellend et al. 2013; Dornelas et al. 2014; Vellend et al. 2017; Dornelas et al. 2019). Plant species regional diversity has increased on oceanic islands and at both large (e.g. US state) and smaller (e.g. British Vice-county) scales on continents (Sax & Gaines 2003). Reptile, amphibian and mammalian species diversity have all increased at the regional scale, with some of the largest increases seen in freshwater fish diversity on oceanic islands, where fish diversity was historically limited by barriers to dispersal (Sax & Gaines 2003). At the local scale, from less than a square metre to a few hectares, the general pattern is more mixed. Plant species diversity is both increasing and decreasing in different locales, resulting in no net change in local diversity (Sax & Gaines 2003; Vellend et al. 2013; Dornelas et al. 2014). Although animal species have not been as well sampled as plants, they present a similar picture, with increases in some areas and decreases in others resulting in the lack of an overall trend in either direction (Sax & Gaines 2003; Dornelas et al. 2014). However, one should note that decreases in the local diversity of plants and animals are seen in areas where land has been converted to a human dominated land type, such as in the conversion of rainforest to palm oil plantation (Fitzherbert et al. 2008). It is also critical to note that, despite stationary/increasing local scale biodiversity, community composition is shifting as species replacement occurs, with potentially significant effects on ecosystem functioning in many areas (Sax & Gaines 2003; Vellend et al. 2013; Dornelas et al. 2014). Given that most organisms, especially plants, tend to interact over small spatial scales, local scale changes in biodiversity may have the largest impacts on ecosystem functioning.

It is worth noting that some authors have concluded that local scale biodiversity is decreasing. Collen et al. (2009) observed a significant decline in terrestrial vertebrate local abundances whilst analysing the Living Planet Index, which is a large database of vertebrate time-series data. Similar results were noted by Newbold et al. (2015), who estimated that there has been a 13.6% decrease in the local scale richness of a taxonomically broad terrestrial assemblage representing 26,953 species. Gonzalez et al. (2016) specifically disputed the findings (no net change in local scale biodiversity) of Vellend et al. (2013) and Dornelas et al. (2014), claiming that statistical and sampling errors led to incorrect conclusions. In a response to this critique Vellend & Dornelas (Vellend et al. 2016) demonstrated that the original conclusions of both papers still stand, although they acknowledged that geographical bias in biodiversity datasets is a problem. There have been far more ecological studies in Europe and North America than on other continents, and so it is difficult to estimate how local biodiversity is changing in under-recorded areas. It may be that the inclusion of local diversity trends from underrepresented regions might alter the overall local scale picture.

With such disagreements in the scientific community, it is evident that further research is needed to ascertain the true overall state of local and regional scale biodiversity changes. Nevertheless, it is clear that local and regional scale biodiversity is increasing in some areas, and may continue to increase as the Anthropocene progresses. Thus, it is important that we develop our understanding of the ecological and evolutionary 'rules' that govern the accumulation of species in novel habitats, just as it is important that we identify the processes that result in extinction.

1.2 Biodiversity in novel habitats

In recent years a number of studies have examined the accumulation of biodiversity in anthropogenic novel habitats (e.g. brown field sites, mine tailings, old fields, and green rooves). The age of a novel habitat can have a significant influence on multiple components of floral/faunal diversity, although effects are not always consistent across different novel habitat types. The species richness, abundance, and/or diversity of multiple taxonomic groups has generally been observed to increase with time since novel habitat creation (mammals, birds, reptiles, and ants in rehabilitated bauxite mined forest - Nichols & Nichols

2003; plants on old agricultural land - Cramer et al. 2008; bacteria on reclaimed coal mine spoils - Li et al. 2014), although plant and arthropod diversity do not appear to increase over time on urban green rooves (Ksiazek-Mikenas et al. 2018). Additionally, there is evidence that native and non-native colonists may be differentially affected by novel habitat age, as increasing time of wheat field cultivation is positively correlated with native weed richness, but negatively correlated with non-native weed richness (Ikegami et al. 2019). This implies that as native species become more adapted to novel habitats they may colonise in greater numbers, potentially outcompeting the non-native species which are typically associated with novel habitats (McKinney 2002; Lugo & Helmer 2003; Bonter et al. 2010).

In addition to hosting more non-native species, community composition in novel habitats is often distinct from that found in pre-existing habitats (Hobbs et al. 2006; Jones & Leather 2012; Tischew et al. 2014), and novel habitats sometimes support rare native species by replicating the environmental conditions of distinctive natural habitats (Eversham et al. 1996; Colding & Folke 2009; Dvorak & Volder 2010). However, uncertainty remains over the degree to which novel habitats can truly support native biodiversity, and the quantitative extent to which non-native species associate with novel versus pre-existing habitats.

Whilst many authors examine the effects of novel habitat age, or employ categorical comparisons of pre-existing and novel habitats, none attempt to quantify the degree of 'novelty' that is provided by a novel habitat. Furthermore, research may be constrained by the potentially unique nature of each novel habitat type, making it difficult to generalise about differences in the accumulation of species in different novel habitats. In the following section I introduce a model system that has potential to overcome both of these issues: the study of insect communities on non-native plants.

1.3 Non-native plants as novel habitats

Non-native plants are now present in high numbers and diversity in all regions across the globe (van Kleunen et al. 2015), and are playing an increasingly important ecological role in most landscapes (Schlaepfer et al. 2011). Non-native plants are largely dispersed to new areas through human agency (van Kleunen et al. 2015), thus functioning as anthropogenic novel habitats for the invertebrate communities that associate with them. Non-native plant

habitats are abundant, highly replicated (as plant individuals and species), and important ecologically, making them an ideal model system to better our understanding of how species associate with, and accumulate in, novel habitats in general. The extent to which a plant species captures the various aspects of habitat will of course vary across invertebrate trophic levels and with insect specialism. Higher trophic levels are less likely to be closely associated with individual plant species, and the same applies to generalists at all trophic levels (Harvey et al. 2010; Bezemer et al. 2014). There are also certain aspects of habitat that are not determined by plant species identify, such as site-specific biotic and abiotic conditions, and the composition of surrounding plant communities. However, there are many other aspects of habitat that plant species identity can effectively capture, with plants presenting specific abiotic and biotic conditions, such as varying chemical composition, architecture (e.g. size, branching complexity, surface and interior composition, and appearance), microclimate (e.g. moisture, temperature, and light intensity), phenology, and associated microbial and faunal communities (Strong et al. 1984; Schoonhoven et al. 2005).

Under the proposed framework I focus on several quantifiable plant traits that have parallels in other novel habitat types. By influencing a variety of structural, chemical, and phenological traits, host plant phylogenetic isolation may operate as a proxy for the habitat novelty provided by different plant phenotypes – from the perspective of potential insect colonists. This is evident in the strong phylogenetic signal present in the host range of many herbivorous insects (Novotny & Basset 2005; Weiblen et al. 2006; Gilbert et al. 2015). Host plant phylogeny is a determinant of various structural traits that are ecologically relevant for insect-plant interactions, such as leaf toughness, water content, evergreeness, and area (Pearse & Hipp 2009). Furthermore, by impacting plant architecture phylogeny also affects within-plant microclimate (as various factors associated with within-plant microclimate, such as light penetration, airflow, and temperature, are inherently influenced by plant structure – e.g. Devakumar et al. 1999). Phylogenetic proximity between plants also correlates with similarity in the diverse array of chemicals present in their tissues (e.g. leaf phenolics, tannins, and protein content - Pearse & Hipp 2009) and secondary metabolites (Wahlberg 2001; Wink et al. 2010). Finally, closely related plants typically present similar phenologies, and tend to flower and leaf at similar times (Davies et al. 2013).

The divergent structures of non-native plants mirror the physical and micro-climactic diversity of other novel habitats (such as mine tailings or urban heat islands), the variety of

chemicals that they produce is analogous to the chemical and soil diversity of post-industrial sites, and their differing phenologies reflect the seasonal biotic and abiotic changes in other novel habitats types. Given that such a variety of traits determine habitat novelty it can be difficult to quantify the relative 'novelty' provided by other types of anthropogenic novel habitats, whereas phylogeny provides a convenient proxy for novel plant habitats.

In addition to phylogeny, I propose that the time that a non-native plant has existed in a region/locale is comparable with the time that a novel habitat has existed. Finally, a non-native plant's range size, and its spatial relationship with the ranges of the other plants around it, is analogous to the size and location of a novel habitat in relation to surrounding habitats, which may act as biological 'sources' of colonising species.

The rest of this chapter will primarily focus on how phylogeny, time, and geography impact insect diversity on non-native plants. The main emphasis will be on herbivorous insects, as this represents the vast majority of the literature.

1.4 The effects of non-native status and phylogenetic isolation

Several hypotheses have been proposed to explain the varying success of non-native plant introductions, with success determined by a lack of associated herbivorous insects, and by minimal competition with other plants (for brevity from this point onwards herbivorous insects and mites will be referred to simply as herbivores). According to the well-established and substantiated Enemy Release Hypothesis, non-native plants invade successfully as they are freed from coevolved herbivores in their introduced range, and so experience decreased herbivory (Williams 1954; Maron & Vila 2001; Meijer et al. 2016). The Novel Weapons Hypothesis is essentially an extension of the Enemy Release Hypothesis to include competing native plants as well as native herbivores. It posits that toxic secondary plant compounds (allelochemicals), such as those found in root exudates or sap, exhibit more potent effects in a plant's introduced range, inhibiting the competitive abilities of neighbouring native plants as well as defending the incomers from the attacks of native herbivores (Callaway & Ridenour 2004; Harvey et al. 2010). Conversely, the Biotic Resistance Hypothesis explains how non-native plants might fail to invade new areas where there are strong biotic interactions with native herbivores limiting their ability to establish and spread.

However, unlike the Enemy Release and Novel Weapons Hypotheses, evidence for the Biotic Resistance Hypothesis is conflicting, and there is little evidence that herbivory limits the spread of non-native plants in their introduced range (Maron & Vila 2001), possibly because those that experience high levels of herbivory fail to establish at all, and hence are not studied in non-native locations.

A wealth of studies and reviews have examined how herbivore biodiversity differs on non-native plants compared with native relatives (e.g. Kennedy & Southwood 1984; Lewinsohn 2005; Spafford et al. 2013; Bezemer et al. 2014). Most studies approach the issue categorically, although with recent advances in DNA sequencing some authors are now including a plant's phylogenetic isolation in their analysis (Pearse & Hipp 2009; Spafford et al. 2013; Branco et al. 2015). Although there are exceptions, on average a non-native plant will be more phylogenetically isolated in its introduced range than it was in its native range. The functional and biochemical distinctiveness of phylogenetically isolated plants is probably one of the driving factors behind differences in the associated herbivores of native and non-native plants, as determined by Grandez-Rios et al. (2015). In order to validate this assumption, and to tease apart the effects of non-native status and phylogenetic isolation, it is essential that researchers incorporate both non-native status and phylogenetic isolation in their analyses. If this is not possible, then authors should at the least employ a triplet experimental design, with native plants compared with both congeneric and non-congeneric non-native plants (Zuefle et al. 2008; Burghardt et al. 2015; Kirichenko & Kenis 2016; Salisbury et al. 2015; Salisbury et al. 2017). Almost all studies sampling native and non-native plants approach the problem with simple pair-wise contrasts (native vs. non-native), whilst a triplet design provides a proxy with which to consider the effects of host phylogenetic isolation in the absence of a continuous measure.

The five measures commonly sampled when comparing herbivore communities on native and non-native plants are species richness, species abundance, herbivore damage, the β-diversity of herbivores between native and non-native plants, and herbivore specialisation. Two different approaches are commonly applied when sampling. Most studies either use a biogeographical approach (sampling a plant in its native and non-native ranges), or a community approach (sampling native and non-native plants in the same community). The most robust conclusions emerge when non-native plants are sampled using both methods,

but applying both is often not realistic, meaning that researchers usually employ one or the other (Meijer et al. 2016).

1.4.1 Species richness

Research suggests that herbivore species richness is often decreased on non-native plants, particularly if non-native plants are phylogenetically isolated from the native flora (Spafford et al. 2013; Grandez-Rios et al. 2015). The phylogenetic isolation of native plants is also negatively correlated with herbivore richness, strengthening support for the effect of phylogenetic isolation (Vialatte et al. 2010). However, Branco et al. (2015) concluded that a non-native plant's overall phylogenetic isolation had little influence on herbivore richness, and that the presence of congeneric native plants in the introduced range was the most significant predictor. This highlights that the role of phylogenetic isolation may only operate at certain levels of the phylogeny. Interestingly, some studies have found no difference in herbivore richness between native and non-native plant species (Zuefle et al. 2008), or have found increased richness on non-natives compared with native relatives (Novotny et al. 2003; Sugiura et al. 2007; Harvey et al. 2013). Disparate results such as these highlight the need for more detailed investigation into the relationship between richness, native status, and phylogenetic isolation, and so I examine these issues further in **Chapter 3** and **Chapter 4**.

1.4.2 Abundance

Herbivore abundance is generally decreased on non-native plants compared with their native relatives (Bezemer et al. 2014; Meijer et al. 2015; Meijer et al. 2016), and comparison of herbivore abundance on non-natives in their introduced and native ranges typically reveals decreased abundance in the introduced range, supporting the Enemy Release Hypothesis (Liu & Stiling 2006). Importantly, non-native plant species with congeneric native relatives in their introduced range support increased herbivore abundance compared with non-natives that have no close native relatives (Kirichenko & Kenis 2016; Salisbury et al. 2017), and abundance is reduced on phylogenetically isolated native plant species (Vialatte et al. 2010). These studies highlight the importance of considering the phylogenetic isolation of a non-native plant when sampling herbivore abundance, analyses of which are notably absent from the literature. It is important to note that similar or increased abundance has been found on non-natives in some studies (Novotny et al. 2003; Harvey et al. 2013;

Salisbury et al. 2017), since even a single herbivore species can be abundant, and herbivores colonising a non-native plant could themselves experience a degree of escape from their natural enemies. Given these conflicting findings, and the absence of studies investigating the relationship between abundance and phylogenetic isolation, further investigation is required. The influence of host plant native status and phylogenetic isolation on associated insect abundance is considered in **Chapter 3**.

1.4.3 Herbivory

The overall picture for herbivore damage is quite unclear. Bezemer et al. (2014) reviewed 10 meta-analyses and case studies and revealed that while some authors concluded that non-native plants suffer decreased levels of herbivore damage, others found no difference in damage. Some studies have even revealed increased levels of herbivore damage on non-native plants compared with co-occurring natives (Harvey et al. 2013; Fan et al. 2016). Such mixed results lead to the conclusion that release from insect herbivory is not always empirically supported for non-native plants in introduced areas, and mirror the conflicting trends observed in herbivore richness and abundance on non-native plants. Whilst I do not investigate herbivore damage per se in this thesis, herbivore abundance and damage are often linked (von Sydow 1997; Hartley et al. 2010), and herbivore abundance is considered in **Chapter 3**.

1.4.4 β-diversity, community distinctiveness, and herbivore specialisation

The consensus is clearer for β-diversity, with the majority of studies agreeing that phylogenetic proximity between native and non-native plants is positively correlated with the similarity of their herbivore communities (Gossner et al. 2009; Burghardt & Tallamy 2015; Grandez-Rios et al. 2015; Lin et al. 2015). Many authors have examined this issue with pairwise contrasts of host plants. In **Chapter 3** I take a new approach, and examine the influence of host plant phylogenetic isolation and native status on the overall distinctiveness of the insect communities associated with individual plant species (compared with all of the other plants within an assemblage).

Contrasts of the ratio of specialist to generalist herbivores reveal that specialists often fail to colonise non-native plants (Lewinsohn et al. 2005; Brändle et al. 2008; Spafford et al. 2013), although colonisation by specialists is more common when non-native plants are more closely related to the native flora (Bezemer et al. 2014). This seems logical, as less

isolated non-native plants generally present less divergent morphologies and chemistries, making colonisation by specialist herbivores (without the need to evolve novel adaptations) more likely. Studies specifically relating herbivore specialism to plant phylogenetic isolation are lacking from the literature, and those that have analysed the effect on specialism present conflicting findings. Grandez-Rios et al. (2015) concluded that more phylogenetically isolated non-native plants host a more specialised herbivore fauna, and that plant origin had no effect on specialisation. Brändle & Brandl (2001) examined the effect of native plant taxonomic isolation, and reached the same conclusion. These results contrast with the conclusions of Vialatte et al. (2010), who determined that more phylogenetically isolated native plants host more generalised herbivore communities. In **Chapter 4** I examine the relationship between insect specialisation, insect/plant non-native status, and host plant phylogenetic isolation.

1.5 The effect of time

It is generally agreed that the length of time that a non-native plant has existed in a region is positively correlated with herbivore species richness (Kennedy & Southwood 1984; Brändle et al. 2008; Kirichenko & Kenis 2016). As time passes herbivores have more chances to encounter a non-native plant and to colonise it, and to develop specialised adaptations to facilitate this colonisation. Despite general agreement on the presence of the richness-time relationship there is debate in the literature as to its exact nature. Some authors have concluded that the effect of time reaches an asymptote during the first few centuries following establishment, after which further increases in species richness are better predicted by the size of the area that a non-native plant occupies, rather than by the duration of time that it has been there (Strong 1974; Strong et al. 1977). Kennedy & Southwood (1984) agreed that the effect of time does slow as the pool of potential colonists (those that have not already colonised) becomes depleted, although they posited that richness will continue to rise at a very low rate thereafter, as a function of both area and time. Brändle et al. (2008) concurred that richness does not reach an asymptote within a few hundred years, and that both area and time have an effect. In contrast, Banerjee (1981) observed a richness asymptote in as little as 30 years on tea in north-east India. This finding differs from most other studies, and highlights that the species of plant in question and the

exact circumstances of introduction may have large influences on the rate of herbivore accumulation.

Carpenter & Cappucino (2005) concluded that herbivore damage on non-native plants is not correlated with time since introduction. Similarly, Andow & Imura (1994) found unconvincing support for a correlation between herbivore richness on non-native plants and time. Harvey et al. (2013) substituted space for time, and sampled herbivore abundance, richness, and damage on a non-native plant at various distances from its invasion front. Abundance and richness were positively correlated with time since introduction, whilst damage was negatively correlated. The authors suggest that non-native plants may become better defended against local herbivores over time, meaning that damage reaches a maximum soon after introduction. An alternative explanation might be that herbivores themselves experience a temporary period of escape from their own natural enemies. This finding contrasts with other studies that have found a positive relationship between time and herbivore damage (Siemman et al. 2006). This might seem more intuitive, but it again emphasises the context-dependence of events.

Time since introduction and total recording effort are usually positively correlated. The positive relationship between species richness and recording effort (the species-accumulation curve) is a very well-established phenomenon (Fisher et al. 1943). This means that in order to truly test the effect of time statistical models must control for the effect of recording effort. This is especially important given that a plant's rarity might influence sampling by entomologists. Following introduction, and depending on their invasive capabilities, non-native plants might be expected to be relatively rare for some time, meaning that the true richness of associated herbivores during those early years post-introduction might be under sampled.

To conclude, there is considerable debate in the literature over the effect of time since non-native plant introduction on associated herbivore richness and damage. Furthermore, many of the studies investigating the effect of time were conducted in the 20th century. In **Chapter 3** I revisit the issue with modern analytical and statistical techniques, and consider the effect of time on insect species richness, whilst controlling for recording effort. I include both categorical (archaeophyte non-natives introduced prior to 1500 versus neophyte non-

natives introduced since 1500) and continuous (introduction date of neophyte non-natives) measures of time, enabling me to contrast the effect of time across different scales.

1.6 The effect of space

There are three primary reasons why a non-native plant's range size is expected to be positively correlated with herbivore richness (Kennedy & Southwood 1984; Hawkes 2007). A larger range results in an increased encounter rate by potential colonists, it leads to a positive shift in the equilibrium between herbivore immigration and extinction, and it provides a greater variety of niches via increased habitat heterogeneity (a more widely-distributed plant is likely to grow in a wider variety of climates and habitats). The entomologist-area effect is also worth noting as a potential influence on herbivore richness (Connor & McCoy 1979). Larger areas may have more entomologists sampling plants within them, thus biasing sampling effort towards plants with larger ranges, and potentially inflating the species-area effect. Nonetheless, the species-area effect is well grounded, and many studies have confirmed its presence for both native and non-native plants (Strong et al. 1977; Kenendy & Southwood 1984; Lawton et al. 1993; Andow & Imura 1994; Brändle & Brandl 2001; Brändle et al. 2008; Branco et al. 2015). In **Chapter 3** I build upon these studies, and investigate if host plant range size and phylogenetic isolation operate in tandem to influence herbivore species richness, whilst controlling for recording effort to account for the entomologist-area effect.

The species-area (or volume) effect also applies on the scale of individual plants, with tree height (for native species) positively correlating with herbivore richness (Kennedy & Southwood 1984; Brändle & Brandl 2001). The same explanations as for the species-area relationship apply here. Larger trees have an increased encounter rate with potential colonists, they can sustain larger herbivore populations that are more resilient, and they provide increased habitat heterogeneity to support a wider range of herbivores. These rules are also likely to apply for non-native plants. However, surprisingly few studies include a measure of plant architecture in their analysis, although experiments are often designed to account for plant architecture (e.g. Burghardt & Tallamy 2015). In addition to the plant-size (volume) effect, there is also a clear abundance-area effect. Salisbury et al. (2017; 2019) found that the canopy cover of non-native plant beds was positively

correlated with the abundance of a variety of different plant-inhabiting and soil-surface-active invertebrate functional groups, and that accounting for canopy cover improved the fit of their overall models. The same findings were replicated with pollinators and flowering units on non-native beds in a separate study on the same plots (Salisbury et al. 2015). Whilst these findings may seem like common sense, they highlight the need to account for plant architecture both in the design of experiments and also in the statistical models used to reach any conclusions.

1.7 Non-native plants and pollinators

Just as contrasts of herbivore diversity on native and non-native plants often reveal differing trends, insect pollinator associations with non-native plants may also vary. Comparisons of flower visitation rates present a mixed picture, as pollinator visitation may be increased (Powell et al. 2011), similar (Harmon-Threatt et al. 2009), or decreased (Hochkirch et al. 2012) on non-native plants compared with congeneric native plants. Taking a biogeographical approach, Brown & Cunningham (2019) revealed that non-native crop plants are visited by fewer bee genera outside of their region of origin, with native crops supporting more bee genera than non-native crops in most biogeographic realms. Differences in flower morphology and phenology, or in the quality and quantity of the nectar produced by native and non-native plants may explain some of the differences in flower visitation (Chittka & Schürkens 2001; Bezemer et al. 2014; Carvalheiro et al. 2014). This emphasises the need to account for nectar and pollen resource availability both physically (e.g. flowering units, flower structure, and nectar chemical composition) and temporally (i.e. days/weeks/months in flower) when sampling pollinators on native and non-native plants.

Contrasts of pollinator diversity between habitats invaded by non-native plants versus non-invaded habitats also reveal contrasting patterns. Impacts on pollinators are often negative, for example, bee species richness and abundance increases in riparian forests following the removal of non-native Chinese privet (*Ligustrum sinense*) (Hanula & Horn 2011), and the richness and abundance of entire pollinator communities is lower in meadows invaded by the goldenrods *Solidago canadensis* and *Solidago gigantea* (Moroń et al. 2009). However, there are cases where pollinator richness (Bartomeus et al. 2008; Bartomeus et al. 2010) or abundance (Nienhuis et al. 2009) is similar in invaded habitats. This suggests that non-native

plants may not always negatively impact pollinator α-diversity. Nonetheless, it is important to consider that similar levels of richness or abundance could mask underlying alterations to pollinator community composition, as pollinator groups may be differentially affected by non-native plants (Goodell 2008; Fenesi et al. 2015; Salisbury et al. 2015).

Whilst the associations of pollinators with non-native plants are well studied, very few authors include non-native plant phylogenetic isolation in their analyses (e.g. Morales & Traveset 2009; Carvalheiro et al. 2014). It is thus unclear whether non-native plant phylogenetic isolation affects pollinators in a similar manner to herbivores. Similar impacts might be expected given that the phylogenetic distance between plants correlates with floral phenotypic distance (Morales & Traveset 2009), although the strength of certain effects may vary, as pollinators are typically more generalised than insect herbivores (Fontaine et al. 2009). In **Chapter 3** I contrast the effects of host plant native status and plant phylogenetic isolation on the richness, abundance, and composition of a community of relatively generalist pollinators versus a community of relatively specialised plant-inhabiting insects.

1.8 A Multitrophic Perspective

As evidenced in this chapter, there is a wealth of information in the literature about insect herbivore (and pollinator) diversity on non-native plants. However, herbivores are only a part of the diverse multi-trophic invertebrate communities associated with non-native plants. For this reason, several recent reviews have proposed that we must expand the bi-trophic focus if we are to fully understand how invertebrate communities colonise non-native plants (Harvey et al. 2010; Spafford et al. 2013; Bezemer et al. 2014). It might be expected that individuals in higher trophic levels follow similar trends to those followed by herbivores. Natural enemies of herbivores also rely on chemical and visual cues associated with food plants to locate their hosts or prey, and so should be influenced by the phylogenetic isolation of non-native plants in a similar way to herbivores (Harvey 2010). This pattern is generally evident in studies that have included higher trophic levels in their analyses. In their review, Spafford et al. (2013) concluded that total arthropod community richness is reduced on non-native plants compared with native plants, with the degree of the reduction relating to the phylogenetic distance between native and non-native plants.

Similarly, predators (excluding Aranea) were more abundant on native plots compared with congeneric and non-congeneric non-native plots (Salisbury 2017). Aranea were not influenced by plant origin; the abundance of hunting Aranea was significantly predicted by plant architecture, whilst the abundance of web-spinning Aranea was not. Just as the diversity of herbivore functional groups can be differentially affected by a plant's architecture, groups in higher trophic levels may also be diversely affected.

Effects on the diversity of higher trophic levels are not necessarily the same as for herbivores. Fortuna et al. (2013) found that whilst the herbivorous lepidopteran *Pieris brassicae* preferred to oviposit on a native host plant, its parasitoid did not discriminate between herbivore-induced plant volatiles produced by the native plant and a non-native plant. Likewise, Salisbury (2017) found that Aranea did not discriminate between native and non-native plant beds. In cases where predators and parasites do not discriminate but herbivores do discriminate this could lead to a shift in the ratio of predators and parasites to prey and hosts. Increased attack by natural enemies might deplete herbivore numbers on non-native plants, contributing to the success of non-native plants under the Enemy Release Hypothesis (Williams 1954), and to the decreased herbivore diversity found on non-native plants in many cases (e.g. Kennedy & Southwood 1984; Lewinsohn 2005; Meijer et al. 2016). Conversely, it is also plausible that a non-native plant might be less attractive to the natural enemies of herbivores (Harvey 2010). In this case, non-native plants would attract an increased ratio of herbivores to higher trophic levels compared with native plants. This might contribute to the failure of non-native plants to successfully invade as posited by the Biotic Resistance Hypothesis (Maron & Vila 2001), and to the conclusions of some researchers that certain non-native plants host increased herbivore diversity compared with natives (Novotny et al. 2003; Sugiura et al. 2007; Harvey et al. 2013). It is possible that some of the discrepancies in the literature as to the direction of diversity trends when comparing natives and non-natives are driven by higher trophic levels, suggesting that further research taking a multitrophic approach is needed. In **Chapter 3** I investigate how the richness, abundance, and community distinctiveness of insects from multiple trophic levels is influenced by host plant native status and phylogenetic isolation.

1.9 Native and non-native insects on non-native plants

When studying insect accumulation on non-native plants few authors consider whether the insects themselves are native (insect native status). The global rate of insect introductions to new regions is increasing (Seebens et al. 2017), mirroring trends seen in other animal groups such as birds, amphibians, reptiles, and mammals (Hulme et al. 2009; Blackburn et al. 2015). Given the increasing prominence of non-native insects on a global scale, there is remarkably little information about the ecological mechanisms that determine their accumulation in both pre-existing and novel habitats. Whilst the processes that determine the spread of certain ecologically or economically concerning species are well studied, such as with the harlequin ladybird *Harmonia axyridis* in Great Britain (Roy & Wajnberg 2008) and the emerald ash borer *Agrilus planipennis* in the USA (Muirhead et al. 2006), few authors contrast the associations of multiple non-native insect species with native and non-native plants. Some non-native insect species associate primarily with non-native plants (Sugiura et al. 2007; Rodríguez et al. 2019), and non-native plant area is a strong predictor of spatial patterns of non-native insect establishment (Edney-Browne et al. 2018). However, there is evidence that non-native insects also rely on native plants, as regional native plant richness is a strong predictor of insect invasions (in addition to non-native plant richness - Liebhold et al. 2018).

The majority of insect introductions globally are linked to the ornamental plant trade (Kenis et al. 2007; Smith et al. 2007; Liebhold et al. 2012), meaning that garden centres and domestic gardens are the likely establishment sites for most new insect arrivals. By studying the host plant associations of insects in gardens, we can gain a valuable insight into the ecological, temporal, and spatial mechanisms that determine the spread of many non-native insect species. We can also inform the conservation of native insects, as gardens are increasingly recognised as a significant resource for native wildlife in Great Britain and across the globe (Smith et al. 2006; Goddard et al. 2010; Soanes et al. 2019). Through their associations with plants in gardens, native insects inevitably interact with many non-native plants, as non-native plants are in the majority in gardens (Loram et al. 2008). There is some indication that certain groups of native insects rely heavily on non-native plants in the absence of native hosts/food plants, including urban butterflies (Shapiro 2002; Jones & Leather 2012; Ramírez-Restrepo et al. 2017) and honeybees in suburban ecosystems (Koyama et al. 2018). In **Chapter 4** I investigate whether some native insect species are

uniquely associated with, and thus supported by, non-native plants in both gardens and the wider landscape. I also contrast the native/non-native plant associations of native versus non-native insects in gardens, and native insects in gardens versus native insects in the wider landscape, whilst considering factors such as a host plant phylogenetic isolation, non-native host plant age (arrival pre 1500 versus post 1500), insect specialism, and non-native insect origin.

1.10 Thesis rationale and outline

Regional (national scale) diversity is generally increasing during the Anthropocene, whilst local diversity presents a mixed picture. Increases in local and regional diversity may be facilitated by the creation of anthropogenic novel habitats, which allow species to establish in new locales/regions without necessarily displacing native species. Non-native plants are increasingly widespread and important ecologically, and most would not exist in Great Britain if not for human agency, making them an ideal model system to better understand the accumulation of species in anthropogenic novel habitats. Despite decades of insect-plant research there is still considerable disagreement in the literature as to the strength of certain predictors (e.g. native status and time since non-native plant introduction) and, in many cases, there is even confusion as to the direction of effects on different metrics of insect diversity (e.g. richness and abundance). Furthermore, many authors overlook important aspects of insect-plant interactions such as host plant phylogenetic isolation, insect native status, and insect community composition and distinctiveness.

Studies of insects on non-native plants are commonly framed from the perspective of invasive species control, or in the context of insect-plant community ecology, whereas I frame my research in the novel context of anthropogenic species accumulation at local and regional scales. In the following chapters I take a multipronged approach, and examine the host plant associations of native and non-native insects in gardens and the wider landscape, employing a combination of experimental and analytical approaches to synthesise the data from local-scale experiments and two geographic-scale insect-plant databases. In **Chapter 2** I present the Database of Insects and their Food Plants (DBIF), and the Royal Horticultural Society Advisory Database (RHS), and outline the steps I have taken

to clean and update the datasets for publication, thus enabling wider accessibility, and consequently increased engagement from the scientific community. In **Chapter 3** and **Chapter 4** I present the results of my own experimental work and analyses of the data within the DBIF and the RHS. I investigate multiple aspects of insect diversity (richness, abundance, and community distinctiveness), and consider the influence of various predictors on insect-plant associations, including host plant and insect native status, host plant phylogenetic isolation, time since non-native plant introduction, host plant range size, ecosystem novelty (novel garden ecosystems vs. the wider landscape), non-native insect geographical origin, and insect specialism. Finally, in **Chapter 5** I highlight my most significant findings, discuss potential avenues for future research, and place my findings into the wider context of biological conservation in a rapidly changing Anthropocene world.

Chapter 2 Documenting a century of invertebrates on plants in Britain: The RHS and the DBIF

Gall midge (Cecidomyiidae) slide collections at the Natural History Museum

The Royal Horticultural Society plant health and entomology centre

2.1 Abstract

The variety and complexity of the chemical and structural environments provided by plants is one of the driving factors behind the evolution of the rich invertebrate diversity on Earth today. Understanding more about phytophagous invertebrate and plant associations is vital to improve our knowledge of fundamental ecological interactions and processes, and is necessary to inform the conservation of both invertebrates and plants. Despite high public and scientific interest in recording invertebrates on plants, research is often limited by the size and/or breadth (taxonomic, spatial, and temporal) of invertebrate-plant interaction datasets.

I present 138,642 records of primarily phytophagous invertebrates associating with plants over the past century in gardens and in the wider landscape, hosted within two geographic-scale datasets that focus primarily on Great Britain: The Royal Horticultural Society Entomology Advisory Database (RHS), and the Database of Insects and their Food Plants (DBIF). Collectively, these data represent one of the largest sources of British invertebrate-plant interactions that is currently available, and can contribute to a wide array of research in diverse fields, such as global change biology, macroecology, conservation biology, and a range of ecological topics (e.g. population, community, network, and evolutionary ecology).

All invertebrates and plants are included with current nomenclature, and with full taxonomic information (family, order, and higher classifications, and taxonomic authorities). I provide the feeding type of all invertebrate species, and the native status (i.e. native versus introduced at different dates) within Great Britain of all invertebrate and 'higher' plant species included in the database. Spatial and temporal information is available for most garden records (RHS), and dated literature sources are available for all records from the wider landscape (DBIF).

2.2 Introduction

Phytophagous invertebrate and plant interactions are at the foundation of many food webs, with the majority of invertebrates at all other trophic levels (e.g. detritivores, predators, and parasitoids) also associating with and depending on plants, and upon the herbivores that develop and feed on those plants (Schoonhoven et al. 2005; Bezemer et al. 2014; Salisbury et al. 2017; Padovani et al. 2020). Elucidating the various mechanisms (e.g. phylogenetic, temporal, and spatial) that underpin phytophagous interactions is vital to better our understanding of an array of fundamental ecological and evolutionary processes. This is particularly important as invertebrate and plant communities are being rapidly altered by the mass movement of non-native species to new regions across the globe (Roy et al. 2012; Thomas 2013; Seebens et al. 2017). Many invertebrate-plant interactions have been documented in the scientific and non-scientific literatures, however datasets are often limited in size and taxonomic, geographical, and/or temporal breadth due to the practical constraints of studying ecological interactions.

To overcome this issue I tap into the rich tradition of natural history recording in Great Britain, collating data that was collected by both experts and the wider public at a regional scale. Collectively, the Royal Horticultural Society Entomology Advisory Database (RHS) and the Database of Insects and their Food Plants (DBIF – Ward 1988; Smith & Roy 2008; Ward et al. 2019) present 138,648 interactions between primarily phytophagous invertebrates and plants recorded mostly in Great Britain. Our data include both native and non-native invertebrates and plants that were sampled in a variety of habitats, including both gardens and the wider landscape. The data span more than a century of recording, and comprise of records from across the country. Both datasets have already contributed to a variety of original research including i) the role of host plant native status, phylogenetic isolation, and geographic range size on the diversity and distinctiveness of phytophagous insect communities (DBIF; Padovani et al. 2020), ii) the differing host plant associations of native and non-native insects in gardens and the wider countryside (**Chapter 4**), iii) insect species' distribution and host range changes (RHS; e.g. Salisbury & Malumphy 2017; Plant et al. 2019; Tuffen et al. 2019; DBIF; e.g. Quinn et al. 1997; Quinn et al. 1998; Stewart et al. 2015), and iv) the evolutionary history of phytophagous insects (and mites) and of their food plants (DBIF; Ward et al. 2003). Additionally, the DBIF was

used to populate the iSpot wildlife recording social network prior to opening it up to public input (Pocock et al. 2016; https://www.ispotnature.org/).

The RHS reports 78,420 interactions between 1,271 primarily herbivorous invertebrate taxa and 1,829 plant taxa, mostly recorded in gardens in Great Britain (and Ireland/Northern Ireland – 236 records) from 1905 to 2018. Records were submitted by members of the public to the Royal Horticultural Society Gardening Advice Service, and identified by entomologists who logged the interactions in the database. Invertebrate and plant taxa are identified to as close to species level as was possible with the information available. Interactions record invertebrate taxon *x* associated with plant *y* and do not include abundance information. Dates are reported for all records, and spatial location data are available for most records at the 100km^2 resolution (for finer resolutions of up to 100 m^2 and records from 2019 onwards please contact the Royal Horticultural Society (A. Salisbury) to discuss potential collaboration).

The DBIF reports 60,222 interactions between 7,511 primarily herbivorous insect (and mite) species and 5,057 plant taxa, recorded primarily in the wild in Great Britain and Europe from 1891 to 2009. Interactions are reported from a wide variety of sources, including field guides (e.g. Heath & Emmet 1979) and entomological journals (e.g. The Entomologists Gazette). All invertebrate taxa are recorded at the species level. Plant taxa are reported at the taxonomic resolution present within the source data. Interactions represent invertebrate taxon *x* associated with plant *y* and do not include abundance information. A suite of additional attributes is available for many records (e.g. invertebrate life stage, invertebrate habitat, and invertebrate pest status).

The DBIF is available at http://www.brc.ac.uk/dbif/, although the data hosted there are not downloadable as a complete dataset. The data presented here have been cleaned (e.g. for nomenclature changes and synonyms), and I have added information on whether the invertebrates and plants are native or introduced to Great Britain. For a full list of publications involving the DBIF see http://www.brc.ac.uk/dbif/DBIFreferences.aspx. The RHS was not previously publicly available, although the Royal Horticultural Society have made the data available to various authors. See **Appendix 1A** for a full list of all publications associated with the RHS.

2.3 Methods

2.3.1 The RHS

The Entomology section of the Royal Horticultural Society Garden Advice Service has kept records since 1905. The Entomology section provides advice to Royal Horticultural Society members, including identification of the invertebrate fauna present in their gardens. Interaction data are submitted in various forms (phone, e-mail, letter, and in person, for example at the Chelsea and Hampton Court Flower Shows) to the Entomology Advisory team, who identifies the invertebrate involved, relays the information back to the interested party, and records the interactions within the database. See https://www.rhs.org.uk/membership/rhs-gardening-advice for an overview of the current service. I include records from 1905-2018 in our dataset. See **Fig. 2.1** for the distribution of RHS records across Great Britain. See **Table A1.1** for the interaction description variables associated with each RHS record.

Invertebrate specimens were provided to the Royal Horticultural Society Entomologists for 24,778 (~32%) records. Photos were provided for 2,115 (~3%) records, and illustrations for 31 (<1%) records. No sample was provided for 30,879 (~39%) records. Invertebrate identification for these records relied on Entomologist expertise, and was based upon a description of the invertebrate and the identity of the host plant. For example, a red beetle feeding on the foliage of *Lilium* would be diagnosed as lily beetle (*Lilioceris lilii*). In 20,623 (~26%) cases the provision of a sample was not recorded within the database. The majority (99%) of these 'Not Recorded' records are from before 1980, after which the record keeping system was overhauled to improve the quality of the data collected.

Within the RHS, 58,109 records (~74%) have British grid references, and 228 records (<1%) have Irish/Northern Irish grid references. There are 18,280 (~23%) records with no location information, 1,815 (~2%) that are certain to have occurred in Great Britain (but without grid references), 7 (<1%) that occurred in Ireland/Northern Ireland (but without grid references), and 218 (<1%) records from overseas.

There are 4,882 records of vertebrates (Amphibians, Birds, Fish, Mammals, and Reptiles) associated with garden plants that are not included in our dataset. To access them please contact the Royal Horticultural Society (A. Salisbury).

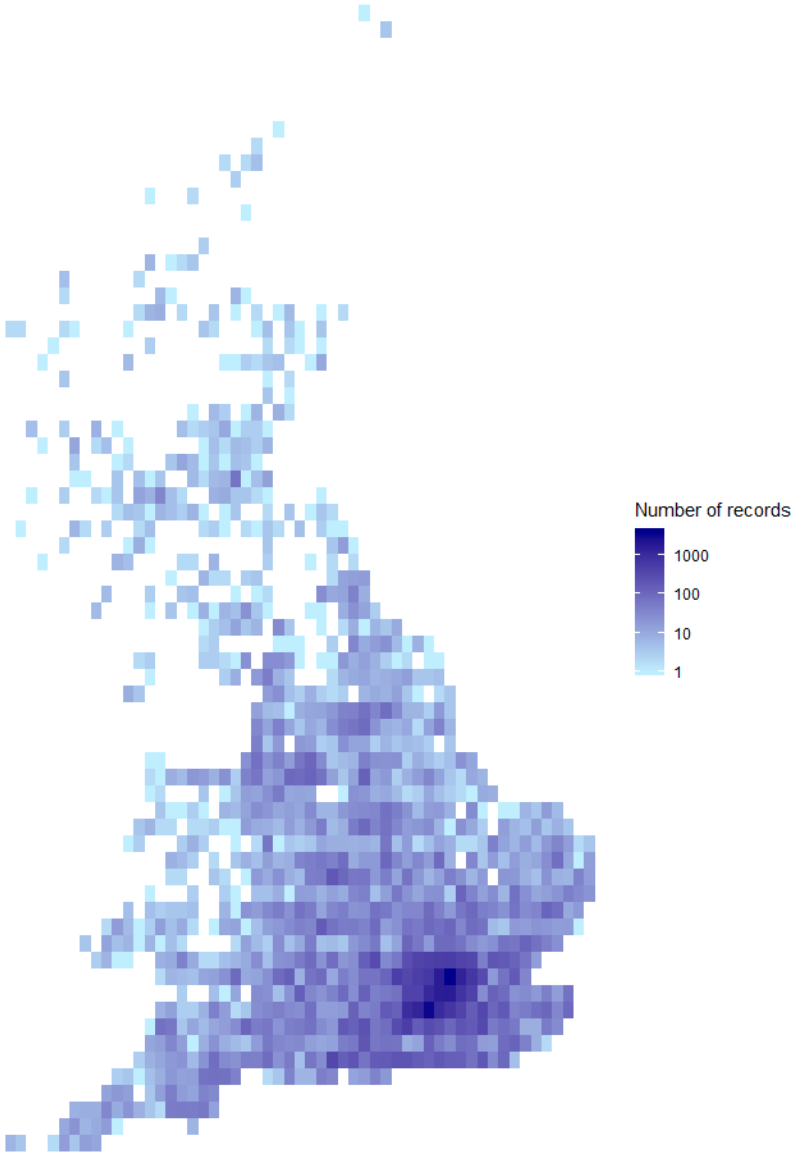

Figure 2.1: The geographical distribution of RHS records across Great Britain. The 58,109 (~74%) records with British grid references are displayed here. 228 (<1%) records with Irish/Northern Irish grid references are not displayed here. There are 18,280 (~23%) records with no location information, 1,815 (~2%) that are certain to have occurred in Great Britain (but without grid references), 7 (<1%) that occurred in Ireland/Northern Ireland (but without grid references), and 218 (<1%) records from overseas.

2.3.2 The DBIF

The DBIF (Ward 1988; Smith & Roy 2008; Ward et al. 2019) was founded on a systematically compiled list of the British herbivorous insect (and mite) fauna. For most taxa, this was assembled from the Royal Entomological Society's series *Checklists of British Insects and Handbooks for the Identification of British Insects*. In an update (2007 – 2008), the invertebrate checklists for some families were updated from new sources (particularly within Coleoptera and Lepidoptera). In such cases, species new to the British fauna were added to the database. Records of interactions were mostly collated from the published literature; sources included books, checklists, journals and private correspondence. The slide collections at the Natural History Museum, London, were consulted for gall midges (Diptera: Cecidomyiidae), scales and mealybugs (Hemiptera: Coccoidea) and thrips (Thysanoptera). To achieve comprehensive coverage, where possible at least one major source was used from both the British and continental European literature for each insect taxonomic group. Groups represented a variety of taxonomic levels, depending on the availability of information within the literature (e.g. group = Thysanoptera [order] vs. group = Nepticulidae [Lepidopteran family]). Major sources were the most recent and comprehensive study of a group, and were identified through consultation with experts.

In addition to recording invertebrate-plant associations, the DBIF includes an array of additional attributes for many records (e.g. invertebrate life stage, invertebrate habitat, and invertebrate pest status). See **Table A1.2** for the interaction description variables associated with DBIF records (availability is dependent on the source literature).

The DBIF primarily focuses on the host plants that invertebrates need for completion of their development, meaning that most records involve immature invertebrate life stages and their associated plants (37,781 records; ~63%). The remaining records involve adults or a mixture of adult and immature invertebrates (13,089 records; ~22%), or have no specified life stage (9,352 records; ~16%). Interactions involving adults include i) adults feeding on the same host as the immature stages (as in hoppers, aphids, and scales), ii) adults feeding on a wider range of related hosts (as in many beetles), and 3) adults feeding on different resources altogether, such as nectar or pollen (as in many butterflies and moths, hoverflies, or thrips). A qualitative assessment of the relative importance of host plants for larval development or adult feeding, in relation to other associated plants, is

provided in the 'InteractionStatus' column (if this information was available in the source literature). 'Important' 'InteractionStatus' would have been assigned to plant *X* in the following hypothetical examples: "Recorded on plant species *X* and also occasionally on plant species *Y* or *Z*"; "*X* is an important host but also found on *Y* or *Z*"; "Usually on host plant *X* and rarely on *Y*".

I have broadly classified all DBIF literature sources into the following categories: 'Field Guide' (39,953 records; ~66%), 'Journal Article' (15,639; ~26%), 'Slide Collection' (2,991; ~5%), 'Other Article' (993; ~2%), 'Other Book' (409; <1%), and 'Private Article' (237; <1%). 'Field Guide' is used in a broad sense, including very general guides (e.g. *A Dipterist's Handbook* – Stubbs & Chandler 1978) and more focused sources such as monographs (e.g. *Flies of the Nearctic Region. Cyclorrhapha II (Schizophora: Calyptratae) Anthomyiidae Volume III* – Griffiths 1984). The 'Field Guide' category also includes checklists and general books on invertebrate ecology (e.g. *Carabid Beetles in their Environments* – Thiele 1977). 'Other Book' demarcates books that are not invertebrate focused (e.g. *Poplars and Willows in Wood Production and Land Use*. *FAO Forestry Series* – International Poplar Commission 1979). 'Journal Article' includes peer-reviewed articles that generally represent primary sources of insect plant interactions (e.g. Nielsen, J. K. (1978) Host plant selection of monophagous and oligophagous flea beetles feeding on crucifers. *Entomologia Experimentalis et Applicata, 24*(3), 562-569). The 'Other Article' category includes magazine articles (e.g. Grant, J. A. (1970) *Countryside, 217*, 301-307), governmental advisory publications (e.g. Wheatley, G. A. (1979) Advisory Leaflet – Ministry of Agriculture, Fisheries, and Food, *68,* 1-11), and conference publications (e.g. Easterbrook, M.A. & Solomon, M.G. (1983) Tenth International Congress of Plant Protection 1983, *1,* 109-109). 'Slide Collection' refers to slide collections housed at the Natural History Museum, London. 'Private Article' denotes primary sources which were not published at the time of data collection, but which were personally verified by L. K. Ward. Primary and secondary sources are demarcated with the 'SourcePrimarySecondary' column. Primary sources include the following categories: 'Journal Article', 'Slide Collection', 'Other Article', and 'Private Article'. Secondary sources include: 'Field Guide' and 'Other Book'.

A subset of DBIF records (38,900; 65%) were expertly verified as reliable by L. K. Ward, and included in previous large-scale analyses (e.g. Ward & Spalding 1993; Ward et al. 2003;

Padovani et al. 2020). I have demarcated these records within the 'LKW' column. Many of the records that have not been expertly verified represent more recent additions to the DBIF (median year of non-verified records = 1992, mean year = 1987; median year of expertly verified records = 1974, mean year = 1968). Additionally, they represent records of invertebrates on rare/casual non-native plants that were not established in the wild. Most records of such plants were excluded during the creation of the 'LKW' subset so that the DBIF would better represent the habits of British insects on plants in a natural setting.

During the compilation of the DBIF records from outside of Great Britain (primarily Europe, with some records from North America and Asia) were used to fill gaps in the British data. These overseas records represent interactions between invertebrates on plants that are likely to occur in Great Britain, but had not been observed at the time of DBIF compilation. Approximately 62% of records (37,184) within the DBIF are confirmed to have occurred in Great Britain. The location of all records is detailed in the 'InteractionLocation' column.

Whilst the majority of DBIF interactions were recorded outdoors (56,557 records; ~94%), a small proportion emerged from captive breeding of invertebrates on plants (3,665 records; ~6%). These records are clearly demarcated by the 'RearedCaptive' column.

2.3.3 The RHS and the DBIF: Taxonomic information

United Kingdom Species Inventory (UKSI) codes, Stace's "*New Flora of the British Isles*" (2010), Kew Plants of the World Online (2019), the Fauna Europaea (de Jong et al. 2014), and the EPPO Global Database (2019) were used to group together plant and invertebrate species listed under different synonyms, and to obtain up to date taxonomic information for all taxa. Due to discrepancies between the various datasets, preference was given to the UKSI when updating synonymy, with the other datasets used primarily to update records of species that were not present in the UKSI. See **Table A1.3** for details of the taxonomic descriptors associated with each record.

2.3.4 The RHS and DBIF: Native status

All invertebrate and 'higher' plant taxa (seed plants and ferns) at a species level resolution were assigned a native status in Great Britain. Native status was not assigned to invertebrate and plant genera (or any less resolved taxa) as genera can often include

species that are both native and non-native to Great Britain. See **Table A1.4** for a description of all plant native statuses, and **Table A1.5** for a description of all invertebrate native statuses.

All invertebrate and plant species were first assigned native statuses and neophyte introduction dates at the full taxon level (including subspecies/variety information) using the established sources listed below in the 'RHS and DBIF: Sources of plant native status' and 'RHS and DBIF: Sources of invertebrate native status and feeding type' sections. All remaining taxa without a native status and with associated subspecies/variety information were then 'upgraded' to the species level, and were assigned a status where possible. I have clearly demarcated where native statuses were matched at the full taxon or species level by assigning statuses to two separate columns ('PlantStatus' and 'InvertebrateStatus' = using full taxonomic information; 'PlantStatusSpecies' and 'InvertebrateStatusSpecies' = taxa upgraded to the species level). All RHS invertebrates were matched at the full taxonomic level (including subspecies/variety information). 70 DBIF invertebrate species (<1% of species/subspecies level taxa) were matched with a status after 'upgrading' to the species level, as were 15 RHS plant species (<1% of species/subspecies level taxa), and 196 DBIF plant species (5% of species/subspecies level taxa).

2.3.5 The RHS and DBIF: Sources of plant native status

Plants were initially classified as archaeophytes (non-native, arrived before 1500), neophytes (non-native, arrived since 1500), or as uncertain natives/non-natives using Stace & Crawley's "Alien Plants" (2015). Neophyte introduction dates were also assigned using Stace & Crawley (2015). A large proportion of the remaining plants were classified as British natives using PlantAtt (Attributes of British and Irish Plants – Hill et al. 2004), with Stace's "New Flora of the British Isles" (2010) confirming 15 additional DBIF native plants that were either not included in PlantAtt, or were listed with an uncertain status. Stace & Crawley (2015) followed a specific set of criteria when determining which non-native plants to include in their list: favouring non-native plants that are established in the wild, and excluding those that have not been recorded since 1986, or have been recorded since but only as very rare 'casuals' or 'survivors'. This means that there are many non-native plants within the RHS and the DBIF that are not present in Stace & Crawley. A number of

these were classified as archaeophytes, neophytes, or uncertain natives/non-natives using PlantAtt.

Once the preceding methods had been applied twice (once on plants with full taxonomic details e.g. subspecies/variety information, and once on any remaining plants 'upgraded' to the species level) all remaining plants were investigated further using Kew Plants of the World Online (2019), with native status determined using the native ranges listed therein. This procedure was also applied twice (once using full taxonomic details, once at the species level). Plants with native status determined via the following method represent either rare natives not listed in PlantAtt or Stace (2010), or non-natives primarily found in horticultural settings and not present in the wild as naturalised or casual plants (and so not listed in Stace & Crawley (2015)). Plants arriving from the New World or outside of the North African/European zone (east of the Ural Mountains) were highly unlikely to have arrived in Great Britain prior to 1500, and so were classified as neophytes. Plants arriving from within the North African/European (west of the Urals) zone but from outside of Great Britain were qualified more simply as non-natives, as it was impossible to determine whether they had arrived before or after 1500. Finally, plants with a British native range were classified as natives.

2.3.6 The RHS and DBIF: Sources of invertebrate native status and feeding type

Invertebrate non-native status was assigned using the Great Britain Non-Native Species Information Portal (GBNNSIP; NNSS 2019). There is no definitive list of British native invertebrates, and so I removed all non-native invertebrates from the UKSI (United Kingdom Species Inventory), and used the remainder to classify invertebrates as native. Any invertebrates not found in either the UKSI or the GBNNSIP were classified with an uncertain native status.

Most DBIF records (59,974, >99%) reported an invertebrate-plant interaction feeding type as determined from the source literature. DBIF feeding types include both broad classifications (e.g. phytophagous, omnivorous, and predacious), more specific information on types of phytophagy (e.g. mining, galling, and rolling), and also some information on feeding behaviours (e.g. gregarious, sheltering, and symbiotic). DBIF feeding types are detailed in **Table A1.6**.

RHS feeding types were not recorded for each interaction during the data submission process. During the data cleaning process RHS invertebrate species were broadly classified as scavengers, detritivores (including fungivores), herbivores, omnivores, parasitoids, or predators. RHS invertebrate species' feeding types were initially assigned using the interactions reported within the DBIF (804 species, ~78%; 46,044 records, ~84% of species level records). A literature search determined the feeding type of RHS invertebrate species that were not found in the DBIF (222 species, ~22%; 8,555 records, ~16% of species level records). If an accurate feeding type was not determinable RHS invertebrates were marked as 'Uncertain' (14 species, ~1%; 16 records, <0.1% of species level records). Feeding type was not assigned to any invertebrate taxa at the genus level or above, as invertebrate genera can contain species of multiple feeding types (e.g. the mirid bug genus *Dicyphus* contains both phytophagous and predatory species). See **Results** for a breakdown of the invertebrate/interaction feeding types within the RHS and the DBIF.

2.4 Results

2.4.1 Taxonomic resolution

See **Table A1.3** for details of the taxonomic descriptors associated with each record. The majority of RHS (54,599 records; ~70%) and all DBIF records involve invertebrates identified to the species/subspecies level. Most RHS plant records are resolved to the genus level (58,944 records; ~75%), followed by plants at the species/subspecies/variety level (18,345 records; ~23%), with remaining plant taxa identified to a mixture of higher taxonomic levels (1,137 records; ~1%). Most DBIF plant records are resolved to the species level (40,694 records; ~68%), followed by plants at the genus level (16,813 records; ~28%), with remaining plant taxa identified to a mixture of higher taxonomic levels (2,715 records; ~5%). See **Fig. 2.2** for a more complete breakdown of the taxonomic resolution of each invertebrate and plant taxon in the RHS and DBIF.

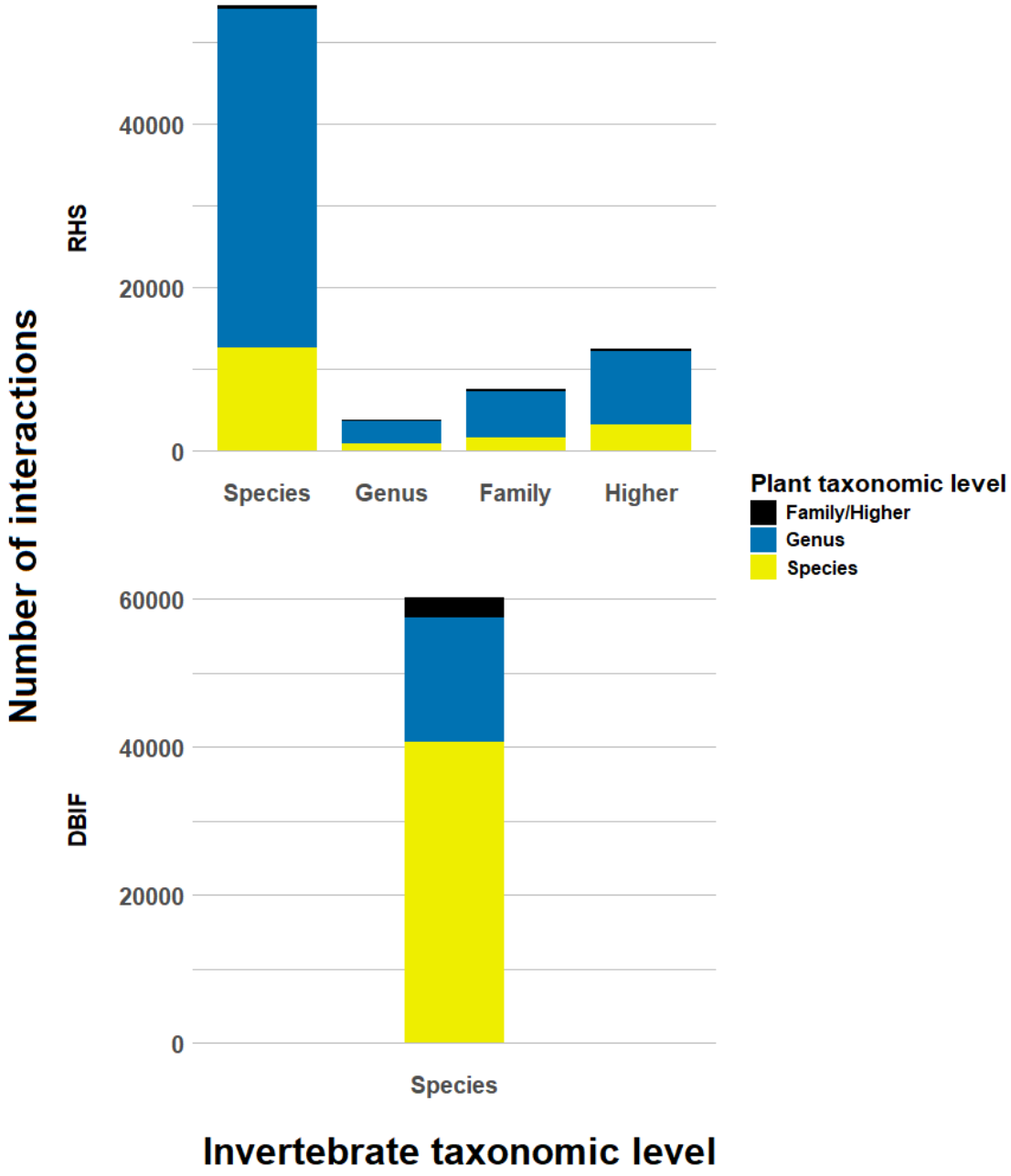

Figure 2.2: The proportion of interactions involving invertebrates and plants at different taxonomic resolutions in the RHS and DBIF. The 'Species' invertebrate and plant taxonomic level includes taxa resolved to the species, subspecies, and variety level. RHS invertebrate 'Higher' taxonomic level includes insect taxa identified to the following resolutions: Superfamily = 5,697 records, Infraorder = 270, Order = 5,677, Subclass = 159, Class = 624, Subphylum = 4, and Phylum = 90). RHS plant 'Family/Higher' taxonomic level includes plant taxa identified to: Order = 2 records, Phylum = 311, Morphological Category = 6 ('Morphological Category' refers to the plant taxon Graminoid). DBIF plant 'Family/Higher' taxonomic level includes plant taxa identified to: Tribe = 13 records, Subfamily = 49, Family = 1,854, Order = 15, Subclass = 53, Class = 68, Phylum = 311, Clade = 26, Group = 298, Kingdom = 28 (Clade refers to the plant taxa Monocotyledoneae and Magnoliidae, and Group refers to the plant taxon Dicotyledoneae).

2.4.2 Taxonomic coverage

Invertebrate higher taxonomic classifications: The RHS consists of a diverse array of invertebrate groups. These are Hexapoda (63,563 records; ~81%), Acari (9,275; ~12%), Gastropoda (2,945; ~4%), Nematoda (1,772; ~2%), Diplopoda (412; <1%), Arachnida (165; <1%), Malacostraca (138; <1%), Annelida (124; <1%), Myriapoda (21; <1%), and Platyhelminthes (11; <1%). The DBIF consists almost entirely of Hexapoda (58,656 records; ~97%), with the remainder of records involving Acari (1,566 records; ~3%).

Invertebrate orders: The five most common invertebrate orders within the RHS are Hemiptera (30,778 records; ~39%), Coleoptera (10,787; ~14%), Lepidoptera (9,912; 13%), Prostigmata (9,005; ~11%), and Diptera (5,241; ~7%). The five most common invertebrate orders within the DBIF are Lepidoptera (23,982 records; ~40%), Hemiptera (12,395; ~21%), Coleoptera (11,379; 19%), Diptera (7,410; ~12%), and Hymenoptera (2,835; ~5%).

Plant higher classifications: The RHS consists entirely of 'higher plants' (seed plants and ferns), and primarily of Angiosperm flowering plants (75,674 records; ~96%), followed by Gymnosperms (2,549; ~3%), and Pteridophytes (203; <1%). The DBIF has a similar overall composition, with the inclusion of some additional non-higher plant/other groups at low frequencies. The DBIF consists of Angiosperms (55,824 records; ~93%), Gymnosperms (3,254; ~5%), Fungi (507; <1%), Pteridophytes (383; <1%), Bryophytes (200, <1%), Chlorophytes (27; <1%), Charophytes (4; <1%), Lycopodiophytes (3; <1%), Marchantiophytes (1; <1%), and Chromista (1; <1%).

Plant orders: The five most common plant orders within the RHS are Rosales (20,709 records; 26%), Ericales (5,296; 7%), Asparagales (4,720; ~6%), Fagales (3,331; ~4%), and Sapindales (3,305; ~4%). The five most common plant orders within the DBIF are Rosales (7,881 records; ~13%), Poales (6,110; ~10%), Fagales (5,878; ~10%), Asterales (5,622; ~9%), and Malpighiales (5,255; ~9%).

2.4.3 Native status

I assigned native status to all invertebrate and plant taxa resolved to a species/subspecies/variety taxonomic level. In the following summary statistics I combine many of the more specific native status categories that are defined in **Tables A1.4 & A1.5**.

See **Fig. 2.3** for an overview of the proportional representation of the various native status categories across the RHS and the DBIF. In summary:

Invertebrate taxa: The RHS is composed of 747 (~73%) native invertebrate taxa, 100 (~10%) non-native invertebrate taxa, and 173 (~17%) invertebrate taxa with an uncertain native status. The DBIF is composed of 6,815 (~91%) native invertebrate taxa, 189 (~3%) non-native invertebrate taxa, and 507 (~7%) invertebrates with an uncertain native status.

Invertebrate records: The RHS includes 32,617 (~60%) native invertebrate records, 11,420 (~21%) non-native invertebrate records, and 10,556 (~19%) records of invertebrate taxa with an uncertain native status. The DBIF includes 53,719 (~89%) native invertebrate records, 1,890 (~3%) non-native invertebrate records, and 4,613 (~8%) records of invertebrates with an uncertain native status.

Plant taxa: The RHS is composed of 134 (~12%) native plant taxa, 924 (~81%) non-native plant taxa, and 78 (~7%) plant taxa with an uncertain native status. The DBIF is composed of 1,019 (~27%) native plant taxa, 2,502 (~67%) non-native plant taxa, and 189 (~5%) plant taxa with an uncertain native status.

Plant records: The RHS includes 1,347 (~7%) native plant records, 15,500 (~84%) non-native plant records, and 1,498 (~8%) records of plants with an uncertain native status. The DBIF includes 26,744 (~66%) native plant records, 12,595 (~31%) non-native plant records, and 1,065 (~3%) records of plants with an uncertain native status.

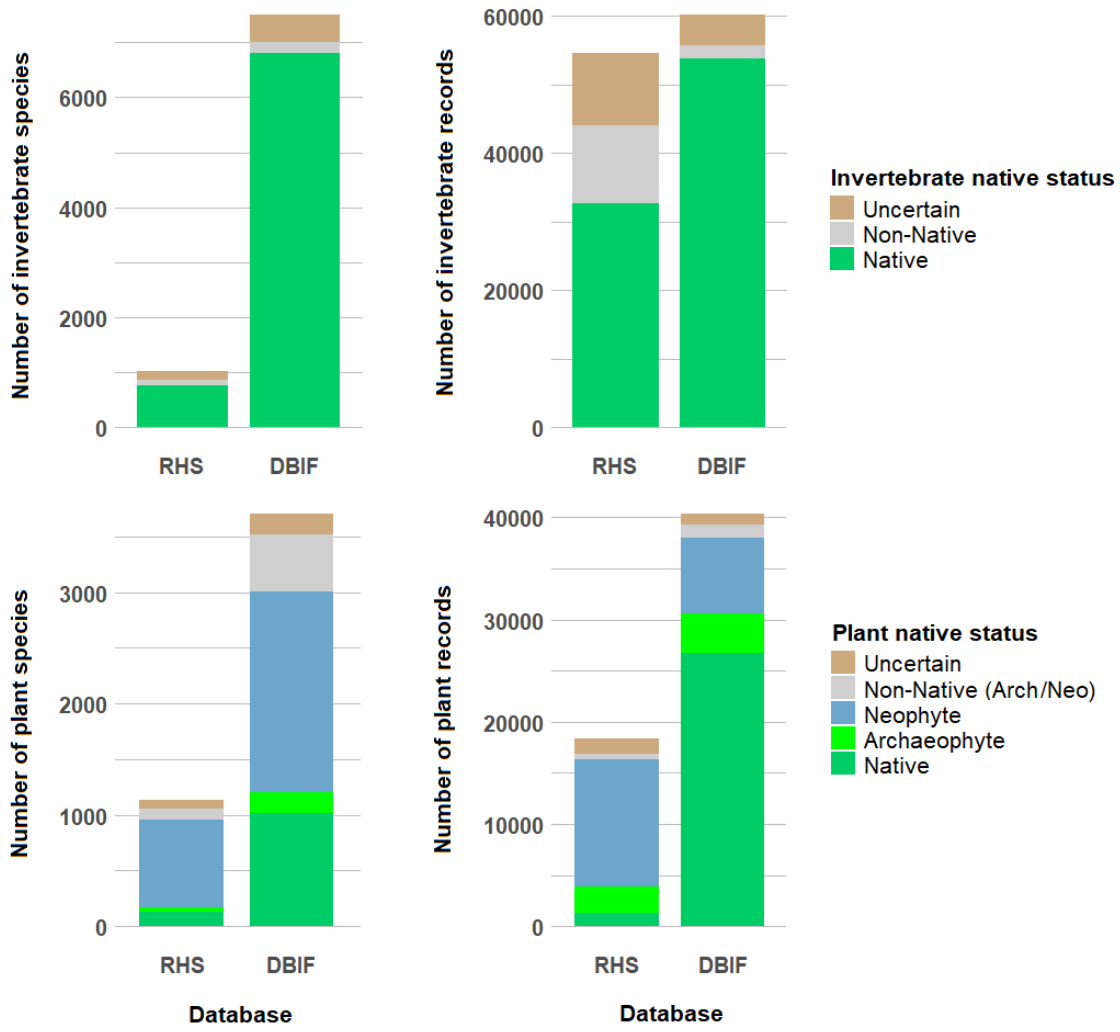

Figure 2.3: Invertebrate and plant native status proportions in the RHS and the DBIF, displayed as the number of species and the number of records. Invertebrate and plant taxa resolved to the genus level or higher were not assigned a native status, and so are not included above (Wisley invertebrates = 245 taxa at the genus level or higher, 23,827 records; DBIF plants = 1,347 taxa, 19,818 records; Wisley plants = 693 taxa, 60,081 records). All DBIF invertebrates were resolved to the species/subspecies level. Invertebrates and plants matched with statuses using full taxonomic information (including subspecies) and those matched with statuses after they were 'upgraded' to the species level (removal of subspecies) are combined above. Several invertebrate and plant native status categories (defined in **Tables A1.4 & A1.5**) are combined above. *Uncertain* invertebrate native status combines the 'Not Found', 'Not Yet Assigned', 'Probably Native', 'Probably Non-Native', and 'Unknown' categories. *Non-Native* invertebrate native status combines 'Non-Native', 'Dependent Non-Native', and 'New Arrival'. *Uncertain* plant native status combines 'Kew No Data', PlantAtt Uncertain', and 'S&C Uncertain'. *Neophyte* plant native status combines 'Kew Neophyte', 'PlantAtt Neophyte and 'S&C Neophyte'. *Archaeophyte* plant native status combines 'PlantAtt Archaeophyte' and 'S&C Archaeophyte'. *Native* plant native status combines 'Kew Native' and 'PlantAtt Native'. *Non-Native (Arch/Neo)* refers to the 'Kew Non-Native' category. See Methods for further details of the invertebrate and plant native status assignment process.

2.4.4 Invertebrate feeding type

DBIF: Interactions were assigned feeding types as described in the source literature. For a full breakdown of all possible DBIF feeding types see **Table A1.6**. Phytophagy is involved in 59,067 records (~98%), 248 records (<1%) do not report a feeding type, and the remainder (907 records; ~2%) involve invertebrates with a mixture of non-phytophagous feeding types (e.g. predacious, omnivorous, saprophagous, and fungivorous).

Approximately a third of phytophagous records (20,251; ~34%) also include additional feeding information, with the vast majority of these records (~99%) reporting more specific details on types of phytophagy (e.g. galling, mining, and webbing) and/or feeding behaviour (e.g. polyphagous, gregarious, ant associated). A small number of phytophagous records also report other non-phytophagous invertebrate feeding types (e.g. predacious, omnivorous, saprophagous, and fungivorous; 265 records; ~1%).

RHS: Invertebrates identified to the species level were assigned feeding types using the DBIF, and with a literature search for any invertebrates not present in the DBIF. The majority of RHS invertebrate species are herbivores (845 species; ~83%), with herbivores involved in 53,557 records (~98% of species level records). The remaining 175 invertebrate species (~17%) are involved in 1036 records (~2% of species level records), and consist of scavengers, detritivores (including fungivores), omnivores, parasitoids, predators, or invertebrates of uncertain feeding type.

2.5 Discussion

2.5.1 General usage notes: RHS and DBIF

Invertebrate and plant native status: When initially assigning native statuses to invertebrates and plants I used all available taxonomic information (including subspecies and variety names). Any taxa at the subspecies/variety level that remained unmatched with a native status were then ‘upgraded’ to the species level before the process was repeated. Therefore, there is a small chance that an incorrect native status may have been assigned to some taxa. For example, it is possible that a non-native subspecies may have been marked as native if the overall species is native in Great Britain. ‘Upgraded’ taxa

represent only a small proportion of the taxa that were assigned native statuses in both datasets (RHS invertebrates = 0%; DBIF invertebrates < 1%; RHS plants < 1%; DBIF plants = 5%), and so there is unlikely to be any impact on analyses involving native status. I have clearly demarcated where native status was assigned to taxa that have been 'upgraded' by assigning statuses to two separate columns ('PlantStatus' and 'InvertebrateStatus' = using full taxonomic information; 'PlantStatusSpecies' and 'InvertebrateStatusSpecies' = taxa upgraded to the species level), enabling upgraded taxa to be easily removed from analyses if there are concerns.

Invertebrate native status: I used the Great Britain Non-Native Species Information Portal (GBNNSIP; NNSS 2019) to assign non-native status to invertebrates within the RHS and the DBIF, and classified any remaining invertebrates that were found within the United Kingdom Species Inventory (UKSI) as natives. The GBNNSIP is recognised as the foremost resource reporting on non-native species in Great Britain, and numerous experts were involved in its compilation (Roy et al. 2012). However, as with any such resource, there are likely to be a few rare or cryptic non-native invertebrates from less well studied groups which are not yet listed in the GBNNSIP. Thus, it is possible that there are some rare non-native species in the DBIF or RHS which are listed as native due to their absence from the GBNNSIP and their inclusion in the UKSI. It is highly unlikely that this will impact most analyses emerging from the data, as the number of incorrect entries will represent a tiny fraction of the native species within the RHS and the DBIF.

Plant native status: I used plant range data listed on Kew Plants of the World Online (POTWO; 2019) to assign native statuses to plants that were unmatched in all of our other sources (see **Methods**). Using POTWO I increased native status matching to cover 94% of RHS plant species, 99% of RHS plant species-level records, 96% of DBIF plant species, and 99% of DBIF plant species-level records. It is possible that plants with a native status of 'Not Found' or 'Kew No Data' have ranges listed in other sources. However, I focused on Kew POTWO as it is the single most comprehensive resource covering all plants (http://www.plantsoftheworldonline.org/about).

2.5.2 RHS usage notes

Uncertain origin records: 23% of RHS records have no location information. It is highly likely that the vast majority of records without location information occurred in Great

Britain, as most RHS members live in Great Britain (RHS overseas membership June 2019 = 2.4%). Furthermore, it is standard procedure within the RHS Advisory service to demarcate all overseas records. 218 records are confirmed to have occurred overseas, and should be removed prior to any analyses focusing on Great Britain.

Distribution of GB records: Users should bear in mind the geographical distribution of RHS records when considering their analyses (**Fig. 2.1**). Whilst records are distributed relatively evenly across Great Britain there is a high density of records from the south east of England, and a paucity of records from some parts of Scotland. This is partially a reflection of the distribution of Great Britain's population over time, but is also due to the location of the Royal Horticultural Society's flagship Wisley garden (in the county of Surrey), and headquarters in central London. Thus, historically much of the membership has been concentrated in the south of England (and primarily in the south east).

Host plant and invertebrate coverage: The RHS is primarily a reflection of the horticultural plant health concerns of members of the British public over the past century, meaning that the data within are not the result of systematic sampling of all garden plants and invertebrates. Common horticultural pests such as aphids, scale insects, and beetles are highly recorded (Aphididae = 7,882 records, ~10%; Coccidae = 6,605, ~8%; Chrysomelidae = 4,742, ~6%), and there are a number of particularly highly recorded interactions of considerable public interest, for example the Scarlet lily beetle *Lilioceris lilii* on lillies (*Lilium* - 2,028 records; 2.6%), the Woolly apple aphid *Eriosoma lanigerum* on apples (*Malus* - 1,522 records; 1.9%), and the Pearleaf blister mite *Eriophyes pyri* on pears (*Pyrus* – 1,017 records; 1.2%).

There is a much higher proportion of non-native plant records in the RHS vs. the DBIF (RHS = 15,500 records, ~84%; DBIF = 12,595, ~31%). This reflects the general floral composition of most British gardens, with 70% of the entire garden flora composed of non-native species (Loram et al. 2008).

Invertebrate feeding types: Given the horticultural focus of the RHS data the vast majority of species level records (~98%) involve phytophagous invertebrates. However, the 'Herbivore' feeding type within the RHS should be viewed primarily as a confirmation of phytophagy, rather than an absolute exclusion of other feeding habits. A literature search was only employed to ascertain the feeding types of RHS invertebrates when they were

not involved in any interactions within the DBIF (222 species, ~22%; 8,555 records, ~16% of species level records). Given that 98% of DBIF records involved phytophagy there are likely to be some RHS invertebrates that are in fact omnivorous, but are listed as herbivores in the RHS due to the absence of additional feeding information in the DBIF.

2.5.3 DBIF usage notes

How up-to-date is the information in the DBIF?: Parts of the database, particularly for Coleoptera and Lepidoptera, were updated (2007-2008) from the most up-to-date monographs available, although these groups may not have been updated with individual species' observations published in amateur journals. For example, numerous Lepidoptera monographs are now more than 10 years out of date, so new information is likely to have appeared. For groups without recent updating interactions will reflect the state of knowledge as at the last source. This is more than 20 years ago for many groups, especially the poorly studied ones. See http://www.brc.ac.uk/dbif/families.aspx for details of when each invertebrate family was last updated. Some backgrounds have recent expert assessments of the condition of the data.

Overseas Records: The DBIF contains 22,065 records (~37%) from outside of Great Britain (primarily from Europe, with some records from North America and Asia) that were included to fill gaps in the British data. If these records are included in analyses it is important to bear in mind that the range of host plants for an invertebrate species is likely to be wider than has been recorded in Great Britain alone. Great Britain holds only a subset of the European flora, and because of the greater area of continental Europe there is more regional variation in host choice. Finally, many herbivores at the edges of their ranges in Great Britain will occupy a wider range of habitats on the continent.

Captive Records: The DBIF contains 3,665 records (~6%) that originated from invertebrates in captivity. It is important to recognise that herbivores will tend to feed on a wider range of plants in captivity than has been recorded in the wild, meaning that plant lists for invertebrates, or invertebrate lists for plants, will be artificially inflated if captive breeding records are included.

Source Types: DBIF data sources were classified into primary and secondary categories. Secondary sources (e.g. field guides, taxon monographs, and checklists) generally compile

data from a wide range of sources, and so may repeat some invertebrate-plant interactions that are reported in primary sources (e.g. scientific journals, amateur journals, and slide collections). Conversely, secondary sources may often include interactions that are not present in any primary sources within the dataset, and may also give a more complete picture of invertebrate-plant interactions across the entirety of an invertebrate's range. I have clearly demarcated primary and secondary sources, and so it is up to the user to consider the pros and cons of including data from both in the same analysis.

Host plant coverage: The DBIF is a reflection of the published literature, and the data within the published literature are not the result of a systematic sampling of host plants. This means that host plants are not sampled evenly for DBIF invertebrate species, and so there are likely to be some invertebrate-plant associations that exist in the wild that are not included in the DBIF.

Invertebrate coverage: The DBIF includes a relatively low proportion of non-native invertebrates compared with the RHS (RHS = 100 [~10%] non-native species and 11,420 [~21%] non-native records; DBIF = 189 [~3%] species and 1,890 [~3%] records); 51 non-native species were recorded in both datasets). This is partially attributable to the close associations between non-native invertebrates and the garden plants that they are largely introduced on (Kenis et al. 2007; Smith et al. 2007), but is also a reflection of the published literature, with the general focus upon specific non-native invertebrates that are ecologically and/or economically concerning.

Invertebrate taxonomic proportions within the DBIF are also influenced by the literature, with this reflected in the preponderance of records of Lepidoptera (23,982 records; ~40%), Hemiptera (12,395; ~21%), and Coleoptera (11,379; 19%). Furthermore, the DBIF focuses solely on insects and mites, meaning that there are many invertebrate groups which are not included in our data.

Invertebrate feeding types: The DBIF is primarily a representation of the habits of the British herbivorous insect (and mite) fauna (~98% of records involve phytophagy). Plants support diverse multitrophic invertebrate communities (Schoonhoven et al. 2005; Bezemer et al. 2014; Salisbury et al. 2017; Padovani et al. 2020), and although the DBIF includes a number of closely associated non-herbivorous species (e.g. predators,

parasitoids, mutualists, or inquilines), there will be many non-herbivorous invertebrate-plant associations which are not found within the DBIF.

2.6 Acknowledgements

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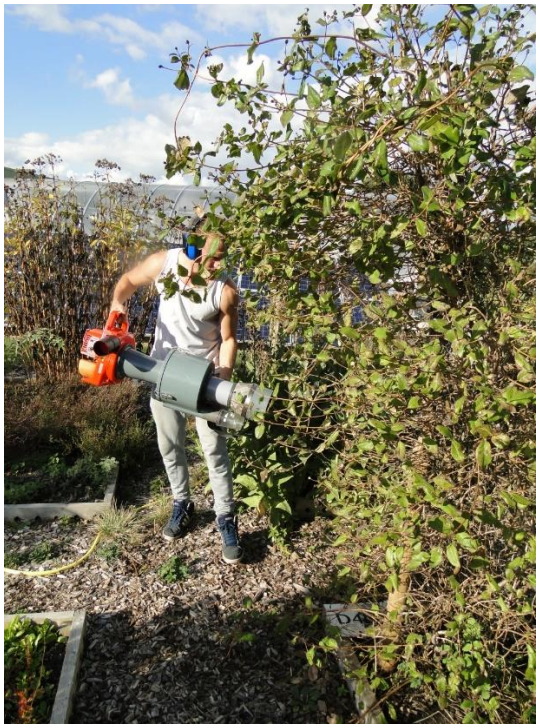
Chapter 3 Introduced plants as novel Anthropocene habitats for insects




Suction sampling and pollinator counts on the Wisley experimental plots

3.1 Abstract

Major environmental changes in the history of life on Earth have given rise to novel habitats, which gradually accumulate species. Human-induced change is no exception, yet the rules governing species accumulation in anthropogenic habitats are not fully developed. Here, we propose that non-native plants introduced to Great Britain may function as analogues of novel anthropogenic habitats for insects and mites, analysing a combination of local-scale experimental plot data and geographic-scale data contained within the Great Britain Database of Insects and their Food Plants. We find that novel plant habitats accumulate the greatest diversity of insect taxa when they are widespread and show some resemblance to plant habitats which have been present historically (based on the relatedness between native and non-native plant species), with insect generalists colonising from a wider range of sources. Despite reduced per-plant diversity, non-native plants can support distinctive insect communities, sometimes including insect taxa that are otherwise rare or absent. Thus, novel plant habitats may contribute to, and potentially maintain, broader-scale (assemblage) diversity in regions that contain mixtures of long-standing and novel plant habitats.

3.2 Introduction

New physical environments and unprecedented mixtures of species arriving from different geographic origins are progressively generating novel ecosystems (Hobbs et al. 2006; Radeloff et al. 2015; Evers et al. 2018) during the Anthropocene, the proposed geological epoch of humanity. The establishment of species in new abiotic and biotic environments may explain why biodiversity is typically increasing at a regional scale, whilst often relatively stable locally (with both gains and losses) and declining globally (Sax & Gaines 2003; Loh et al. 2005; Thomas 2013a,b; Vellend et al. 2013; Dornelas et al. 2014; Thomas 2015; Vellend et al. 2017; Dornelas et al. 2019). Thus, it is important to understand the ecological and evolutionary 'rules' that govern the accumulation of species in novel situations, just as it is important to identify the processes that result in extinction. Studies of brown field sites, mine tailings, old fields, and green rooves have investigated the extent to which novel habitat biotas differ from those of pre-existing habitats (Hobbs et al. 2006; Jones & Leather 2012; Tischew et al. 2014), and have demonstrated that the age of a novel habitat can influence species richness, abundance, specialism, and community composition (Nichols & Nichols 2003; Cramer et al. 2008; Li et al. 2014). However, research is constrained by the potentially unique nature of each novel habitat, and hence there is difficulty generalising about the differences seen in the accumulation of species in different types of novel habitats.

We suggest a new model system in order to achieve replication among habitat types: the association of "insect" (including some mites) faunas with introduced plants in two datasets (from local-scale experiments and a geographic-scale database), where each introduced plant species is hypothesised to represent a different novel habitat for insects, in the regions to which the plants have been introduced. The degree to which a plant species captures all aspects of habitat may vary across trophic levels and with insect specialism (i.e. higher trophic levels may be less closely associated with individual plant species, likewise for generalists at all trophic levels – Harvey et al. 2010; Bezemer et al. 2014), and there are aspects of habitat that cannot be determined by plant species identity (i.e. the composition of surrounding plant communities, and site-specific biotic and abiotic conditions). However, we suggest that plant species identity may effectively capture many aspects of habitat, with plants typically presenting specific abiotic and biotic conditions, such as varying microclimate (e.g. moisture, temperate, and light intensity),

chemical composition, architecture (e.g. size, branching complexity, surface and interior composition), phenology, and associated faunal and microbial communities (Strong et al. 1984; Schoonhoven et al. 2005).

Non-native plants are increasingly prominent in landscapes around the world (Van Kleunen et al. 2015), and are now recognised to have potential conservation value due to their provision of multiple ecosystem services (Schlaepfer et al. 2011), such as the hosting of complex, multitrophic, insect communities (Harvey et al. 2010). Previous comparisons of insects (mainly herbivores) associated with native and non-native plants have generated conflicting results, in which herbivore species richness, abundance, biomass, and damage to plant tissues can be lower, similar or even higher on the non-native plants (Strong et al. 1984, Novotny et al. 2003; Agrawal et al. 2005; Carpenter & Cappuccino 2005; Hawkes 2007; Brändle et al. 2008; Sugiura et al. 2008; Ando et al. 2010; Dostál et al. 2013; Harvey et al. 2013). Some of this variation can potentially be explained by the fact that non-native plants differ in the extent to which they are distinct from native plants. This distinctiveness emerges from differing host plant phenotypes, with these differences determined in part by the phylogenetic relationship between introduced plants and native plant species, which influences how similar they are across an array of phenotypic traits that affect how insects associate with a plant (e.g. olfactory attractants, toxic secondary plant compounds, phenology, and physical structure – Schoonhoven et al. 2005; Cappuccino & Arnason 2006; Rasmann & Agrawal 2011; Bezemer et al. 2014). This has primarily been considered in relation to whether an introduced plant is a close relative of (e.g. in the same genus as) a native species (Branco et al. 2015; Burghardt & Tallamy 2015; Salisbury et al. 2015; Kirichenko & Kenis 2016; Salisbury et al. 2017), but phylogenetic distinctiveness (our proxy for the novelty of a new plant habitat) is more complex than a binary congeneric/non-congeneric classification. When quantified as phylogenetic isolation (Mya), phylogenetic distinctiveness can affect the diversity of insects on both native (Vialatte et al. 2010) and introduced plants (Grandez-Rios et al. 2015) by influencing their phenotype. Thus, phylogenetic isolation is a convenient proxy for the degree of novelty.

In addition to the ‘degree of novelty’ of a novel habitat, it is also important to consider its age (hypothesised as the length of time that a non-native plant has existed in a region), and its geographic extent (analogous to the range size of a non-native plant). As the range size of an introduced plant increases over time, more potential colonists are likely to

encounter it and develop specialised adaptations, potentially generating a positive correlation between the time since arrival of non-native plant species and insect herbivore species richness (Kennedy & Southwood 1984; Brändle et al. 2008; Kirichenko & Kenis 2016). However, the effect of time is not always apparent (Andow & Imura 1994; Carpenter & Cappucino 2005) and may be overshadowed by the effect of range size once a time-richness asymptote is approached (Strong 1974; Strong et al. 1977; Banerjee 1981; Kennedy & Southwood 1984). Host plant range size has a well-established influence on the species richness of insects found on both native and non-native plants (Strong et al. 1977; Kenendy & Southwood 1984; Lawton et al. 1993; Andow & Imura 1994; Brändle & Brandl 2001; Branco et al. 2015). However, there may be differences in the strength of the effect between natives and non-natives (Brändle et al. 2008), and it is very rarely considered in tandem with host plant habitat novelty, i.e. in relation to host plant phenotype as influenced by the phylogenetic isolation of non-native plants (Branco et al. 2015).

Here, we hypothesise that the extensive insect fauna associated with introduced plants may function a model system for the accumulation of species in novel anthropogenic habitats. We consider several functional groups and trophic levels (herbivores, detritivores, omnivores, predators, and pollinators), because the 'perception of novelty' by colonising insects may vary among functional groups and trophic levels (Ando et al. 2010; Fortuna et al. 2013; Salisbury et al. 2017). We test whether (i) novel plant habitats accumulate the greatest diversity of associated taxa when they show some resemblance to surrounding habitats which have been present historically, and (ii) the recruitment of taxa into novel plant habitats varies among functional/trophic groupings. We also (iii) test whether phylogenetically distinct plants accumulate divergent biological assemblages, and hence (iv) whether this divergence may retain or increase diversity in areas that contain mixtures of long-standing and novel plant habitats. Finally, we test the hypotheses that (v) novel plant habitat age (time since introduction of non-native plants which have been introduced since 1500) and (vi) geographic extent (host plant range size) influence the accumulation of diversity and the composition of biological assemblages. This paper tests these hypotheses at two spatial scales using complementary datasets: an extensive field experiment spanning several years (2010-2016), which examines the insects sampled from 69 garden plant species that vary in their relatedness to the native flora of Great Britain;

and analysis of the insect-plant interactions contained within the Great Britain Database of Insects and their Food Plants (DBIF).

3.3 Methods

3.3.1 Local-scale: The experimental plots

The experimental plots were located on two 25 x 13 m sites (blocks) at Wisley, Surrey, UK; one located within the Royal Horticultural Society's (RHS) Wisley Garden at Howard's Field, and the other at the adjacent Deers Farm. Each site housed eighteen 3 x 3 m plots, and each plot contained 14 plant species, drawn from a total list of 69 plant species typically found in flower gardens in Great Britain. The 69 plant species were organised into 23 species triplets, with a third of the plots containing a mixture of native plant species, a third containing a mixture of non-native species closely related to the natives ('congeners'), and the remaining third of the plots containing a mixture of distantly or unrelated 'exotic' plant species from the southern Hemisphere (see below). There were nine different plant mixtures in total (three of native species; three of congeners, and three of exotics), with each occurring twice at each experimental site. Mixtures were assigned locations on sites using restricted randomisation, ensuring an even distribution of plots along the north-south direction. Species replication (4-12 times across the two sites depending on the species triplet) allowed us to test for the effects of species 'native status' (native, non-native congener, exotic) and phylogenetic isolation. **Appendix 2A and 2B** provide further details on the plot design and maintenance, and **Table A2.1** includes a full list of plant species.

The location of plant species on the plots followed a standardised pattern, and controlled for plant growth forms and architectures. Plant species in the same location on each plot (irrespective of native status) were chosen to be as similar as possible in terms of plant height, density and structure, ensuring that the overall composition of each plot was analogous. Initial planting took place between May 2009 and June 2010 (see **Appendix 2B** for further details).

The three native status categories were defined geographically and taxonomically:

1. Native - A species that arrived in Great Britain without anthropogenic intervention (Pyšek et al. 2004).

2. Congener - A species occurring naturally only in the Northern Hemisphere, but not native or naturalised in Great Britain. They were matched by growth habit with the corresponding native plant in the same experiments. 'Congeners' were usually congeneric (16/23) with this native plant, but in seven instances were confamilial. For simplicity, they are collectively referred to as 'congeners'.

3. Exotic - A species occurring naturally only in the Southern Hemisphere, and not naturalised in Great Britain. They were matched in terms of growth habit with the corresponding native plant, and were not necessarily related to it at any particular taxonomic rank. In three cases exotics were confamilial with the native, but in all other case were more distantly related.

3.3.2 Local-scale: Sampling flower visiting aerial insects (pollinators) on experimental plots

Flower visiting aerial insects (hereafter 'pollinators') were sampled from 2010 to 2013, over four to five sampling days per year, and with a minimum of four weeks between days. Sampling days occurred from March to September, covering the main period of pollinator activity, and under climatic conditions that were favourable to pollinator activity. During each sampling session an expert in insect identification (A. Salisbury) stood at the centre of each of the four sides of a plot for one minute and counted all flying insects that landed on or were already on flowers (four minutes per plot total). Pollinators were identified to species level where possible, although in some cases this was not possible (35 taxa at species level, genus = 5, family = 5, superfamily = 1, infraorder = 2, suborder = 1, order = 5). For further details of the pollinator sampling protocol see **Appendix 2C**.

Floral resource availability was quantified, based on the methodology of Heard et al. (2007), as the estimated number of flowering units (single flower or umbel, spike or capitulum for species with reduced or compound flowers) on each plant species (excluding grasses, ferns and analogous plants) at each sampling session. Estimates were recorded as the median value from one of the following classes: 0, 1-5, 6-20, 21-100, 101-500, and 501-1000. Flowering units > 0 was a requirement for inclusion in statistical analysis.

3.3.3 Local-scale: Vortis sampling of insects on plants (various functional groups) on experimental plots

Plant-inhabiting insects were sampled with a Vortis suction sampler (Arnold, 1994; Burkard Manufacturing Co. Limited, Rickmansworth, Herts, UK) in July 2016. Vortis sampling occurred after 10:00, when vegetation was dry to the touch, and with temperatures greater than 17°C. The two experimental sites were sampled alternately, with sampling sessions rotating between them. Vortis sampling was carried out by sweeping the suction nozzle across half of each individual plant for 30 seconds. Certain plant species had an architecture that made efficient Vortis sampling very difficult (e.g., low-growing plants that would generate soil contamination), and so 24 plant species were excluded from further processing and analysis. For further details of the Vortis suction sampling protocol see **Appendix 2D**.

3.3.4 Local-scale: Vortis plant architecture on experimental plots

Several measures of plant architecture were taken, to account for the potential effects of plant size and complexity on insect species richness and abundance (Kennedy & Southwood 1984; Morse et al. 1985; Brändle & Brandl 2001). All plant architecture measurements were taken within a maximum of eight days following Vortis sampling. The height of each plant was measured directly with a 3-m rule, from the ground to the height at which the main bulk of its canopy terminated. Plant area was measured using one of three methods, depending on the composition of the plots. See **Appendix 2E** for further details. The branching architecture of the median height individual of each plant species was also measured, in order to quantify each species' architectural complexity (Pérez-Harguindeguy et al. 2013). See **Appendix 2E** for further details.

3.3.5 Local-scale: Insect identification on experimental plots

Pollinators were identified *in situ* (see above), whereas frozen Vortis suction samples were identified in the laboratory. To generate a balanced dataset with sufficient statistical power within a one-year identification period, four random Vortis sample replicates were selected for each plant species, and a subset of insect orders were targeted. Targeted orders were chosen on the basis that they included a range of insect functional groups, included species that were mostly > 1 mm in length, and required relatively modest specialised knowledge to identify. Targeted orders were Blattodea (cockroaches),

Coleoptera (beetles), Dermaptera (earwigs), Hemiptera (true bugs), Neuroptera (lacewings) and Orthoptera (grasshoppers and crickets). Individuals were identified to species level wherever possible (88 taxa at species level, genus = 11, subfamily = 2, family = 10, superfamily = 2) and always to a taxonomic resolution that enabled accurate assignment of functional group. Primary works used in insect identification for allocation of functional group (Herbivores, Omnivores, Fungivores/Scavengers [Detritivores], and Predators) can be found in **Table A2.2**. Due to our sampling methodology our data do not include any primarily soil inhabiting insects, or any parasitoids.

3.3.6 Geographic-scale: Database of Insects and their Food Plants summary

The Database of Insect and their Food Plants (DBIF – Smith & Roy 2008; Ward et al. 2019) details 60,290 interactions between primarily phytophagous insect species and plants recorded in Great Britain over the last century, based on a wide variety of sources, including entomological journals (e.g. The Entomologists Gazette) and field guides (e.g. Heath & Emmet 1979). The DBIF interactions represent insect species *x* associated with host plant *y*, rather than standardised abundance information; making it possible to analyse the richness associated with different plant species but not abundance. Nonetheless, the database does include frequency information (numbers of separately recorded interactions between given insect and plant species), meaning that the dissimilarity (distinctiveness) of biotas associated with each plant species could be calculated using Chao-Sorensen 'abundance' methods (see below: 3.3.10 Geographic-scale – Statistical Analysis). We refer to DBIF as 'geographic-scale' because the insect-plant data are scattered records from throughout Great Britain (Area 209,331 km^2), but they are ultimately derived from localised observations, although field guide records are commonly derived from many such observations.

3.3.7 Geographic-scale: Database of Insects and their Food Plants cleaning, native status, and range size assignment

We analysed data on 'higher' plants (seed plants and ferns), using only insect-plant records that were expertly verified as reliable and included in previous large scale analyses (Ward 1988; Ward & Spalding 1993; Ward et al. 1995; Ward et al. 2003). We only included records that were certain to have occurred in Great Britain, and excluded any records originating from captive breeding studies. In order to enable accurate assignment of host

plant native status, arrival date, and range size we transformed the dataset to ensure that all records were at a species level resolution, removing genus level (or above) records (7,362 records; approximately 1/3 of the total), and 'upgrading' all sub-species/cultivar/variety information to the species level. BSBI (Botanical Society of Britain and Ireland) taxon version key codes, Stace's "*New Flora of the British Isles*" (2010), UKSI (United Kingdom Species Inventory) codes, the Fauna Europaea (de Jong et al. 2014), and the EPPO Global Database (2019) were used to group together plant and insect species listed under different synonyms.

Plants were classified as neophyte (non-native, arrived post-1500), archaeophyte (non-native, arrived pre-1500), or native (primarily Holocene colonists). Native status and introduction dates (for neophytes) were assigned to plants from several data sources. Non-native plant status and neophyte introduction date were sourced from Stace & Crawley's "*Alien Plants*" (2015). PlantAtt (Attributes of British and Irish Plants – Hill et al. 2004) was used to identify which plants were native, with Stace's "*New Flora of the British Isles*" (2010) confirming 15 additional native plants that were either not included in PlantAtt, or were listed with an uncertain native status. 78 plant species could not be classified reliably as native, archaeophyte or neophyte, and so were excluded from the analysis. Also excluded were 19 hybrids. The final dataset consisted of 4,397 insect species associated with 679 native plant species, 119 archaeophytes, and 234 neophytes.

We quantified host plant range size to account for its well-established influence on insect species richness (Strong et al. 1977; Kennedy & Southwood 1984; Lawton et al. 1993; Andow & Imura 1994; Brändle & Brandl 2001; Branco et al. 2015). Range size data were provided by O. Pescott, courtesy of the Botanical Society of Britain and Ireland and the Biological Records Centre. Range size was quantified as the number of hectads (10 x 10 km grid squares) that a plant was recorded in between 1987-1999 (within Great Britain including the Isle of Man – vice counties 1-112), which represented a period of intensive recording for the New Atlas project (see Pescott et al. 2018 for further information on BRC plant records). We did not include Irish or European plant records as the majority of insect dispersal occurs within Great Britain (for example, the range size of most British butterfly populations is limited to within Britain – Asher et al. 2001). Plants with no recorded range size information (i.e. species too rare to be detected in the specified period) were assigned a range size value of zero (16 plant species).

3.3.8 Local and geographic-scale: Host plant phylogenetic relationships

Phylogenetic relationships between plants were trimmed from a recently published global phylogeny of vascular plants (Qian & Jin 2016), using the R package pez (Pearse et al. 2015), producing three custom phylogenies (appropriate for the analyses of local-scale pollinators, local-scale Vortis, and geographic-scale DBIF data, respectively). In cases where species were not found in the phylogeny all members of their clade were replaced with a polytomy (local-scale pollinators = 31% of species not found, local-scale Vortis = 33%, geographic-scale DBIF = 17%). 11 plant species could not be assigned a place in the DBIF phylogeny as they belonged to clades not included in Qian & Jin's megaphylogeny, and thus were excluded from any analysis involving host plant phylogenetic isolation. Four phylogenetic isolation measures were calculated:

1) Mean phylogenetic isolation: The mean divergence time (in millions of years) from a plant to every other plant in the phylogeny.

2) Nearest phylogenetic neighbour distance: The divergence time from a plant to its closest relative in the phylogeny.

3) Mean phylogenetic isolation from natives: The mean divergence time from a *non-native* plant to every other *native* plant in the phylogeny.

4) Nearest native phylogenetic neighbour distance: The divergence time from a *non-native* plant to its closest *native* neighbour in the phylogeny

3.3.9 Local-scale: Statistical analysis

Insect taxa were identified to varying taxonomic resolutions, as detailed above. Consequently, richness values represent taxon richness, as opposed to species richness. There were several cases where two taxa in the Vortis data were present on the same plant species but could not be fully distinguished (e.g. Anthocoridae nymph vs. Anthocoris nemorum). In these instances all recorded individuals contributed to total values of abundance on a plant. However, during calculation of richness potentially overlapping taxa contributed only once to the total taxon richness associated with a plant.

The Vortis and pollinator data were in all instances analysed separately, given the different methodologies and that the two sampling protocols were carried out several years apart

(2010 – 2013 vs. July 2016), with a few plant species replacements taking place during the interim period (see **Appendix 2A and 2B**). Insect richness and abundance values represent the summed richness and abundance found on all replicates of each plant species (grouping plots and sites) to reduce zeros and low sample sizes. This was appropriate as plant species plot locations were randomised within sites and balanced across the two sites (which were ~ 154 m apart and shared the same soil type).

Although the design was balanced (this balance was maintained for the Vortis analysis following randomised subsampling, as described above), different numbers of plant individuals, quantities of flower per plant and duration of flowering meant that we needed to control for this source of variation in the pollinator analysis. Flowering units (amount of flower) represented the mean of all replicates of a species and was included in the analysis. A Julian date was also calculated for each sampling event (number of days from January 1st). The median of all sampling Julian dates was included as a measure of phenology for each plant species. Finally, the log of the number of replicates of each plant species was included as a predictor in all pollinator analyses, to account for sampling effort effects stemming from large variation in replication (mean = 72.1 samples per plant species, median = 62, but this ranged from 2-307 replicates). Despite even sampling within the Vortis data plant architectures varied, and so we included both the median volume (area*height) of each plant species and host plant branching architecture in the analysis.

Nine Vortis insect taxa were excluded prior to calculation of community distinctiveness. These taxa were identified to a coarse taxonomic resolution, which precluded their distinction from other taxa resolved to a finer level (e.g. Anthocoridae nymph vs. Anthocoris nemorum). All pollinator taxa were included for calculation of community distinctiveness, as despite varying taxonomic resolution all taxa could be distinguished. Community distinctiveness was quantified in the following way for the Vortis and pollinator data. A pairwise dissimilarity matrix of the insects associated with all plants (that hosted an insect species richness > 0) was created using the Chao-Sorensen abundance-based dissimilarity index, as our data contained a substantial fraction of scarcely abundant species, and classic Jaccard and Sørensen indices often perform poorly in these situations (Chao et al. 2005). The Chao-Sorensen dissimilarity matrix was reduced using non-metric multidimensional scaling (NMDS), which collapses information from multiple dimensions into a few, allowing the data to be more easily visualised and interpreted (Kruskal 1964).

NMDS collapsed the Chao-Sorensen matrix into three dimensions with stress values of less than 0.2 for both the Vortis (stress = 0.161) and pollinator (stress = 0.165) data, indicating a good representation of the data in the reduced dimensions. Finally, the distance was measured from each plant's location in three-dimensional space to the group centroid (co-ordinates 0, 0, 0). This distance represented each plant's value of insect community distinctiveness. This technique has been adapted from similar approaches used to calculate mean β-diversity across a group of sites (by taking the mean distance from each site to the group centroid in NMDS space; Anderson et al. 2006; Myers et al. 2015). The location of each host plant in three-dimensional NMDS space is presented in **Fig. A2.3 & Fig. A2.4**.

The mean levels of insect host specialisation were contrasted between the two datasets (Vortis and pollinator) via the d' index (Blüthgen et al. 2006). The number of interactions that an entity (insect or plant) had with all other available partners (expressed as the proportion of observed links out of those possible) is used when calculating d'. Thus, d' can be interpreted as the deviation of an insect's actual interaction frequencies from a null model which assumes that all plant partners were used in proportion to their availability. Possible d' values range from 0 (perfect generalist) to 1 (perfect specialist).

Vortis insect and pollinator nearest phylogenetic neighbour distance models did not include host plant native status as a predictor because, by definition, natives and congeners within a plant species triplet were almost always congeneric, whilst exotics were always more distantly related. This meant that native status was in effect a categorical approximation of phylogenetic proximity.

We considered statistical associations between predictor variables, but these were generally weak (Kendall Tau-b correlation tau < 0.4) or absent in the pollinator and Vortis models (**Appendix 2F**). Status had a significant effect on host plant median Julian date in the pollinator models ($\chi 2 = 9.21$, $p = 0.010$, d.f. = 2), however median Julian date did not significantly improve the overall pollinator models, and so was not included in the final analysis.

3.3.10 Geographic-scale: Statistical analysis

Values of insect richness represented the summed richness from all sources reporting on a plant species. The log of the number of sources reporting on each plant species was included as a predictor in all analyses, to account for sampling effort effects stemming from large variation in the number of sources (1-64 sources, mean = 6 , median = 3, where a source was defined as an individual article).

Insect community distinctiveness was defined as the Chao-Sorensen abundance-based dissimilarity (we employed the Chao-Sorensen index as the DBIF data contained a high proportion of scarcely abundant species; Chao et al. 2005) between the insect community on a given non-native host and the entire insect pool collectively found on well-sampled native plants (insect richness ≥ 10) within the DBIF all grouped together (the very large variation in insect richness among host plants meant that the NMDS method used for the local-scale analyses could not converge in three-dimensional space for the DBIF data). Only plants that hosted an insect richness ≥ 10 were included (natives = 206 plant species, archaeophytes = 30, neophytes = 26), ensuring that host plants had been sufficiently sampled for dissimilarity analysis. Qualitatively similar results were obtained when the analyses were repeated with the insect pool found on all native plant species.

We accounted for variation in sampling effort (log of the number of literature/data sources reporting insect species on a plant) in all DBIF analyses because this was a strong predictor of insect richness (**Table A2.6**). We also considered associations among predictor variables in the DBIF data (see **Appendix 2F**). Sampling effort was weakly correlated (Kendall Tau-b correlation tau < 0.4) with non-native host plant mean phylogenetic isolation from natives, host plant range size, and neophyte introduction date. Host plant range size and neophyte introduction date were also weakly correlated. Host plant native status was significantly associated with all DBIF model predictors. A potential implication of these associations is considered in the **Results**.

3.3.11 Local and geographic-scale: Statistical modelling frameworks common to both scales

All statistical analyses were carried out in R (R Core Team 2017) using R Studio (RStudio Team 2016). See **Appendix 2G** for full a list of R packages used. The distributions and

nature of data varied somewhat between analyses, resulting in slightly different model formulations.

We used either Poisson or negative binomial regression (depending on data overdispersion, both specified with a log link) for the effects of plant native status, phylogenetic isolation, neophyte arrival date (DBIF only), and range size (DBIF only) on insect community richness and abundance (local-scale only), and beta regression (specified with a log link) to test the effect of all of the above predictors on insect community distinctiveness. Status contrasts were calculated with post-hoc Tukey tests. Only beta regression mean submodel test values are reported in this manuscript: the beta regression mean submodel reports the influence of regressors on the mean of a dependent variable, whereas the beta regression precision submodel quantifies the effect of model regressors on dependent variable dispersion (Cribari-Neto & Zeileis 2010). Models were constructed via addition of predictors of interest, and comparison of models with likelihood ratio tests and AIC values. Good model fit was determined via inspection of diagnostic plots, and via calculation of D^2/pseudo R^2 values. D^2 is the glm equivalent of R^2, and represents the proportion of deviance explained by a Poisson or negative binomial model (Guisan & Zimmermann 2000), whilst pseudo R^2 is the beta regression equivalent of R^2 (McFadden 1973). Predictors included in the best fitting models are detailed in the Results section.

Estimating deviance contributions was complicated by the consistently large effect of sampling effort in two of our analyses (local-scale pollinators = log(replicates), DBIF = log(sources)), so we calculated two measures that incorporated the type I and type II SS (Herr 1986) explained by our predictors of interest.

1) A minimum estimate of the deviance (D) explained by all other predictors after accounting for sampling effort: $D = \frac{type\ II\ deviance\ of\ all\ other\ predictors}{null\ deviance - type\ II\ deviance\ of\ sampling\ effort}$

2) A maximum estimate of the deviance (D) explained by all other predictors after accounting for sampling effort: $D = \frac{type\ I\ deviance\ of\ all\ other\ predictors + type\ II\ deviance\ of\ all\ other\ predictors}{null\ deviance - type\ II\ deviance\ of\ sampling\ effort}$

The type II deviance explained by a predictor was calculated using the Anova function in R (Fox & Weisberg 2019). Type II deviance represents the deviance uniquely explained by a predictor, and type I equates to the deviance shared by a predictor with others. Thus, in

equation 2 the dividend represents the maximum amount of deviance that may have been explained by our predictors of interest, and the divisor is the deviance that remains in the model after accounting for the deviance uniquely explained by sampling effort. We calculated the dividend in equation 2 as follows: dividend = null deviance – residual deviance – type II deviance of sampling effort.

A minimum and maximum estimate of explained deviance were calculated for all Poisson and negative binomial models (insect species/taxon richness and abundance), but were not calculated for beta models (insect community distinctiveness) as beta regression does not have all of the properties of 'classical' GLMs (Cribari-Neto & Zeileis 2010), and so reliable calculation of type II SS was not possible.

3.3.12 Local and geographic-scale: Rarefaction

We created sample-based richness rarefaction curves (methods adapted from Colwell et al. 2012) to evaluate how the diversity of insects associated with native species (pooled) differed from the accumulation of diversity on other categories of plant (e.g. neophytes pooled). We estimated rarefaction confidence intervals by bootstrapping 10,000 times, with a sample classified as a plant replicate for the local scale pollinator or Vortis data, and as a unique data source (normally a single article or other publication) and plant species combination for the geographic-scale DBIF data.

We also implemented a 'combined' rarefaction to represent the accumulation of richness in a mixed community. For the local-scale data, this mixed line displays the rarefaction of the total richness found on all plant replicates, but the geographic-scale DBIF mixed line equalises the number of sources from plants of different native status. Thus, the DBIF line represents a summary of the rarefaction of 200 random samples composed of 1/3 natives, 1/3 archaeophytes, and 1/3 neophytes, with each individual rarefaction bootstrapped 10,000 times, and the upper and lower confidence intervals of the mixed line representing the maximum and minimum 95% confidence intervals from the rarefaction of the 200 random samples.

3.4 Results

The three datasets and the hypotheses tested with them are summarised in **Table 3.1**. Pollinators were sight-recorded from the experimental plots for 23 native plant species (1,939 replicates; pollinator replicates were comprised of plant individuals recorded in different years/seasons), 21 congeners (1,390 replicates), and 20 exotics (1,358 replicates); giving 6,307 individual insects from 54 taxa. Plant individuals/patches (replicates) were Vortis (suction) sampled from the experimental plots for 14 native plant species (total 56 replicates), 13 congeners (52 replicates), and 15 exotics (60 replicates); capturing 2,071 individual insects representing 108 taxa of mixed trophic and functional groups. Within the DBIF geographic-scale database 4,397 insect and mite species were reported interacting with 679 native, 119 non-native archaeophyte, and 234 non-native neophyte plant species.

We found no evidence that insect functional/trophic groups (herbivores, detritivores, omnivores, and predators) responded differently to host plant native status and phylogenetic isolation within the Vortis samples (**Table A2.3**), so all Vortis insects were grouped together for the analyses presented in the following text.

Table 3.1 An overview of the three datasets

	Local-scale pollinators	Local-scale Vortis	Geographic-scale DBIF
Sampling methodology	•Pollinators sampled 2010 –2013 (March – September) •Eight minutes per plot •Pollinators identified on the wing to as close to species level as possible	•Vortis suction sampling of plant-inhabiting insects (July 2016) •30 seconds per plant •Insects identified with keys to as close to species level as possible	•Database detailing interactions reported in both primary and secondary literature (from 1920 onwards)
Native status	•Native •Congener non-native •Exotic non-native	•Native •Congener non-native •Exotic non-native	•Native •Archaeophyte (arrival pre 1500) •Neophyte (arrival post 1500)
No. of plant species	•Total = 64 •Native = 23 •Congener non-native = 21 •Exotic non-native = 20	•Total = 42 •Native = 14 •Congener non-native = 13 •Exotic non-native = 15	•Total = 1033 •Native = 679 •Archaeophyte = 120 •Neophyte = 234
No. of insect taxa	54	108	4397
No. of insect individuals	6,307	2,071	NA
Predictors of interest	•Phylogenetic isolation •Native status	•Phylogenetic isolation •Native status	•Phylogenetic isolation •Native status •Range size •Neophyte arrival date
Controls	•Median flowering units •Median Julian date •Log no. of replicates	•Median volume •Branching architecture	•Log no. of sources
Hypotheses tested	•i – iv (see Introduction) •The experimental plots contained garden plants, and so it was not possible to include time since host plant introduction and host plant range size in the analysis	•i – iv (see Introduction) •The experimental plots contained garden plants, and so it was not possible to include time since host plant introduction and host plant range size in the analysis	•i + iii – vi (see Introduction) •The DBIF data contained primarily herbivores (99% of records), and so it was not possible to include functional/trophic group in the analysis

3.4.1 Insect abundance: Local-scale

The highest insect abundances (total number of insect individuals per plant species, measured by Vortis suction samples and pollinator observations) were associated with native plant species (and the lowest abundances with exotic plants (**Fig. 3.1a, 3.1c; Table A2.4**). Vortis abundance was significantly lower on exotic plants compared to native plants, with the median abundance on exotics being 28% of that on native plant species (**Fig. 3.1c; Table A2.4**). Median pollinator abundance on exotics was 18% of that on native plant species, but outliers meant that there was no significant difference (**Fig. 3.1a; Table A2.4**). Median abundances for non-native congeners were intermediate between that of native species and exotics for both Vortis samples and pollinators (**Fig. 3.1**). Non-native congeners supported marginally higher ($0.05 < p < 0.1$ in post-hoc Tukey tests) pollinator and Vortis sample abundances than the corresponding exotic plants (**Fig. 3.1a; Table A2.4**).

We included additional predictor variables in our models of insect abundance to account for host plant structural characteristics (flowering units per plant for pollinators, and plant volume and branching architecture for Vortis insects), sampling effort (pollinators only - log no. of replicates), and sampling date (pollinators only – due to differences among plant species in their flowering phenologies). Pollinator abundance increased with sampling effort and the number of flowering units per plant species (**Table A2.4**). In contrast, sampling date (median Julian sampling day of each plant species) did not lead to significant improvement of the best model (likelihood ratio test $\chi2 = 1.30$, $p = 0.255$, d.f. = 1), and so was excluded from this and subsequent pollinator abundance models. Sampling dates and replication were fully balanced for Vortis samples (so not included in models), but plant species did differ in their size and architecture. However, neither estimated median plant volume ($\chi2 = 0.61$, $p = 0.435$, d.f. = 1) nor branching architecture ($\chi2 = 0.74$, $p = 0.389$, d.f. = 1) significantly improved the model, and hence plant volume and branching architecture were excluded from all Vortis abundance models.

Native status (native, non-native congener, or exotic) is still a relatively coarse categorical variable, whereas the phylogenetic isolation (measured in millions of years since divergence between plant species) of a non-native congener or exotic may better function as a proxy for the novelty of a non-native plant habitat, from the perspective of potential

insect colonists. Abundances of associated insects declined with phylogenetic isolation for both the pollinator and Vortis samples (**Fig. 3.2a, 3.2c; Table A2.4**), indicating that more divergent plant habitats, on average, support lower insect abundances. However, exact details differed for the two datasets. Pollinators were influenced by host plant relationships with the entire experimental community (mean phylogenetic isolation; **Fig. 3.2a**), whereas insects sampled by Vortis were influenced by host plant relationships with their closest phylogenetic neighbour (nearest phylogenetic neighbour distance; **Fig. 3.2c**). A similar pattern emerged when the phylogenetic isolation of non-native plants from *native* species in the plots was considered, although these effects were only marginally significant (**Table A2.4**). Overall, these results suggest a broader range of host plant sources for pollinators than for other plant-associated insects.

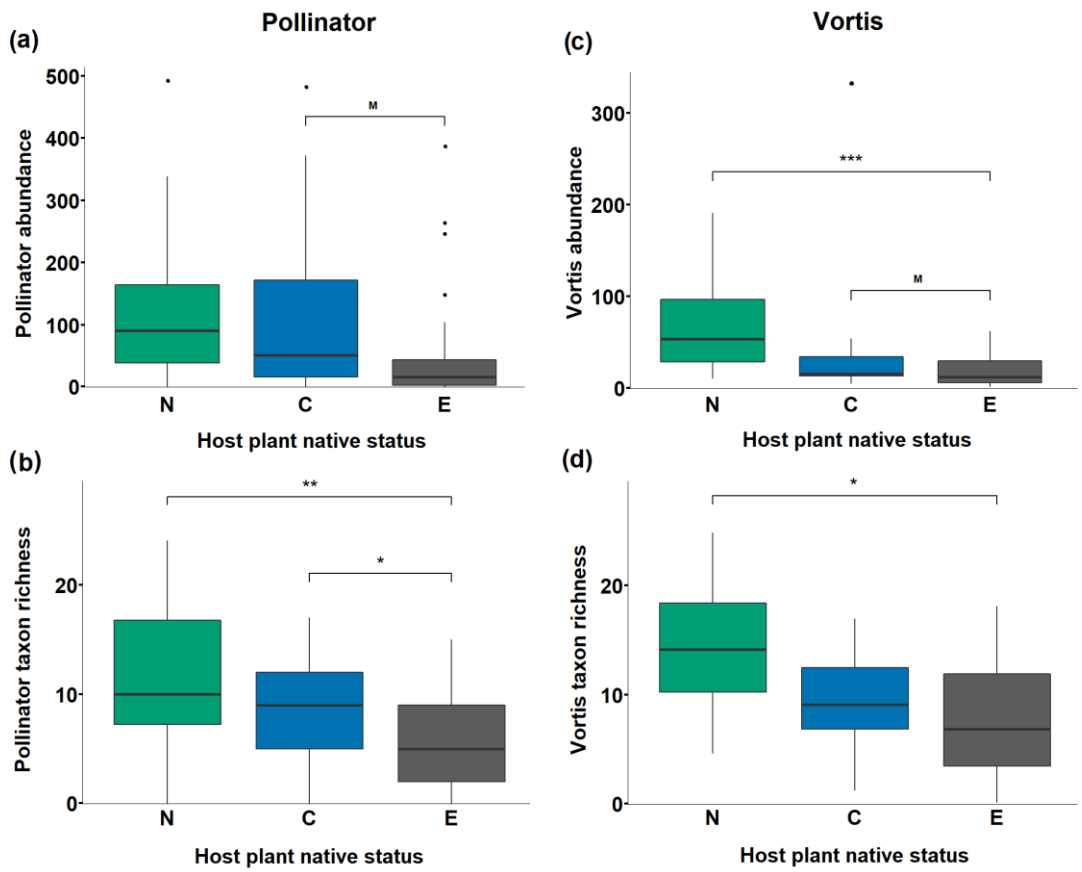


Figure 3.1: Local-scale insect taxonomic richness and abundances associated with native, congener, and exotic plant species. N = native, C = congener, E = exotic. Boxplots represent median, interquartile range, and 1.5x the interquartile range. Points represent outliers. Significance of Tukey post-hoc contrasts M = 'marginal' p of 0.05 < 0.1, * ≤ 0.05, **≤ 0.01, *** ≤ 0.001. D^2 represents the proportion of deviance explained by a model. D represents the range of deviance explained by all predictors of interest, after accounting for sampling effort (log(Replicates)) in pollinator models. See Methods for an explanation of the calculation of D, and of the model building process.

a) Pollinator abundance. Negative binomial model (Pollinator Abundance ~ log(Replicates) + Flowering Units + Status) $D^2 = 0.624$, D = 0.280 – 0.286. Sample size of N = 22 plant species, C = 21, E = 20. **b)** Pollinator taxon richness. Negative binomial model (Pollinator Taxon Richness ~ log(Replicates) + Flowering Units + Status) $D^2 = 0.636$, D = 0.160 – 0.264. Sample size of N = 22 plant species, C = 21, E = 20. **c)** Vortis insect abundance. Negative binomial model (Vortis Insect Abundance ~ Status) $D^2 = 0.205$. Sample size of N = 14 plant species, C = 13, E = 15. **d)** Vortis insect taxon richness. Negative binomial model (Vortis Insect Taxon Richness ~ Status) $D^2 = 0.163$. Sample size of N = 14 plant species, C = 13, E = 15.

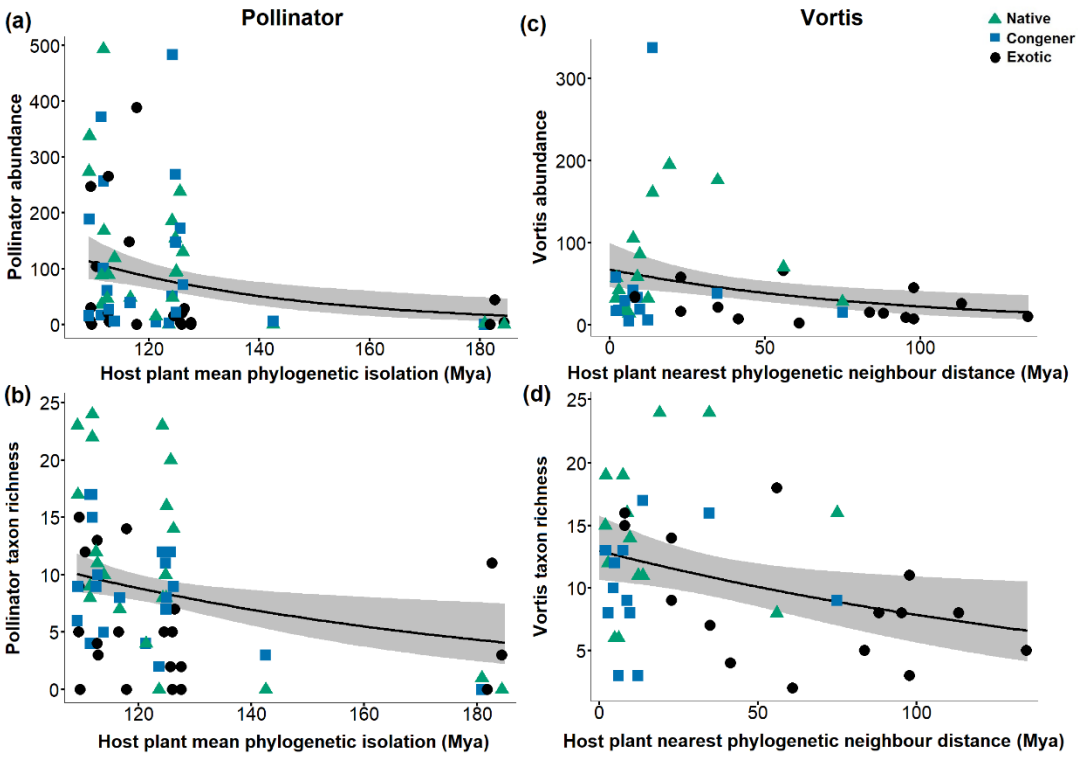


Figure 3.2: The effect of host plant phylogenetic isolation on local-scale pollinator and Vortis insect abundance and taxon richness. Partial regression plots display the effect of our focal predictor (phylogenetic isolation), whilst holding all other predictors at their mean. Shaded areas represent 95% confidence intervals. Data points represent individual plant species. Mean phylogenetic isolation (MPI) = mean distance in millions of years from host plant to all other plants in the local community. Nearest phylogenetic neighbour distance (NPN) = distance in millions of years from host plant to closest phylogenetic neighbour in the local community. See Methods for details of the calculation of D^2 and D.

a) Pollinator abundance. Negative binomial model (Pollinator Abundance ~ log(Replicates) + Flowering Units + MPI) n = 64, p (MPI) = 0.002, D^2 = 0.632, D = 0.209 – 0.381. **b)** Pollinator taxon richness. Negative binomial model (Pollinator Taxon Richness ~ log(Replicates) + Flowering Units + Status + MPI) n = 64, p (MPI) = 0.010, D^2 = 0.671, D = 0.154 – 0.449. **c)** Vortis insect abundance. Negative binomial model (Vortis Insect Abundance ~ NPN) n = 42, p(NPN) = 0.005, D^2 = 0.108. **d)** Vortis insect taxon richness. Negative binomial model (Vortis Insect Taxon Richness ~ NPN) n = 42, p(NPN) = 0.017, D^2 = 0.112. 3.4.2

3.4.2 Insect taxonomic richness: Local-scale

Insect taxon richness (based on pollinator observations and Vortis samples) was highest on native plants and lowest on exotic plants, while the richness associated with non-native congeners was intermediate, particularly in the pollinator samples (**Fig. 3.1b, 3.1d; Table A2.5**). For pollinators, the log of the number of host plant replicates and the number of flowering units were retained as strong predictors in the best models. However, sampling date did not lead to significant improvement of the pollinator richness model ($\chi2 = 0.13$, $p = 0.718$, d.f. = 1), and so was excluded from this and subsequent models. For Vortis samples, neither host plant median volume ($\chi2 = 0.13$, $p = 0.717$, d.f. = 1) nor branching architecture ($\chi2 = 0.11$, $p = 0.745$, d.f. = 1) significantly improved the best model, and thus were not included in any statistical models of Vortis insect richness.

Sample based (number of plant individuals) rarefaction analyses confirmed the significant differences in taxon richness, as shown by the non-overlapping confidence intervals of the curves for exotic and native plants in **Fig. 3.3a & Fig. 3.3b**. Richness was significantly reduced on exotic plants, compared to natives, whilst non-native congeners were again intermediate.

The richness of associated insect taxa also declined with the phylogenetic isolation of host plants for both the pollinator and Vortis samples (**Fig. 3.2b, 3.2d; Table A2.5**). As for abundance, the richness of pollinators on a plant species was influenced by its isolation from the entire plant assemblage (mean phylogenetic isolation; **Fig. 3.2b**), and Vortis insect richness was only influenced by host plant isolation from the most closely related other plant species (nearest phylogenetic neighbour distance; **Fig. 3.2d**). Unlike for abundance, pollinator richness was also impacted by the most closely related other plant (nearest phylogenetic neighbour distance; **Fig. A2.5a**). Similar effects emerged when the phylogenetic isolation of non-native plants from *native* species was considered (**Fig. A2.5b; Table A2.5**), although these effects were mostly non-significant.

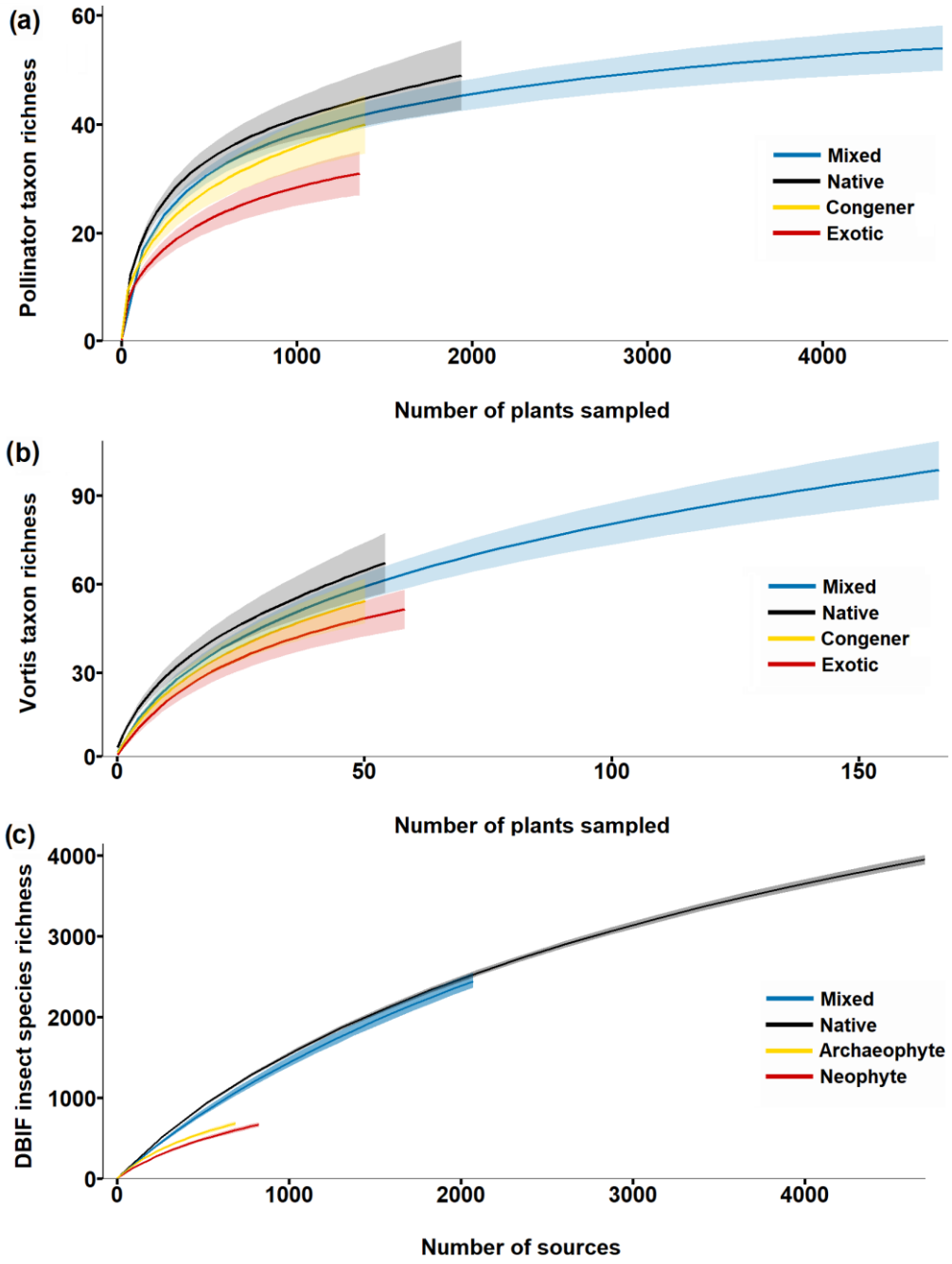


Figure 3.3: Sample based rarefaction of the local-scale pollinator, local-scale Vortis and geographic-scale DBIF data. Shaded areas represent 95% confidence intervals, bootstrapped 10,000 times for each plant type. Vortis and pollinator mixed lines represent rarefaction of the entire dataset. The exception is in (c), where the DBIF mixed line represents the summary of the rarefaction of 200 random samples composed of 1/3 natives, 1/3 archaeophytes, and 1/3 neophytes; the upper bound is the minimum of the 200 upper 95% confidence intervals, and the lower bound is the maximum of the 200 lower 95% confidence intervals. A local-scale sample was defined as a plant species replicate. A DBIF sample was defined as a unique source and plant species combination. Pollinator: sample size of native = 1,941 samples (plant*date*year), congener = 1,390, exotic = 1,358, mixed = 4,689. Vortis: sample size of native = 56 samples (plant), congener = 52, exotic = 60, mixed = 168. DBIF: sample size of native = 4,700 samples (source*plant), archaeophyte = 691, neophyte = 826, mixed = 2,073.

3.4.3 Insect taxonomic richness: Geographic-scale

Rarefaction analyses showed that richness accumulated (with increased sampling effort) at a significantly reduced rate on introduced plants (neophytes and archaeophytes) compared to natives, and that archaeophytes accumulated species at a faster rate than neophytes (**Fig. 3.3c**). Statistical modelling revealed that the species richness of insects increased significantly when introduced plants were closely related to native plant species (for three of the four metrics of phylogenetic isolation), increased significantly with the range sizes of the introduced plants, and increased with DBIF sampling effort (**Fig. 3.4; Fig. A2.6; Table A2.6**). Date of introduction (for neophyte-only models) had no significant effect on insect species richness (**Table A2.6**). Host plant native status (neophytes introduced since 1500, archaeophytes introduced prior to 1500) had a highly significant effect on the richness of the insects found on non-native plants in the DBIF (**Fig. 3.4; Table A2.6**), with archaeophytes hosting more insect species than neophytes. The inclusion of native status in our models led to the loss of the significant effects of two of our four metrics of phylogenetic isolation (non-native plant mean isolation from natives, and non-native plant nearest native neighbour distance). The association of DBIF host plant native status with all other model predictors (see **Appendix 2F**) was the probable cause of this loss of significance.

It was difficult to determine the 'true' deviance (effect sizes) explained by phylogenetic isolation, range size, and native status because of the large effect of sampling effort (which varies greatly among plant species in the DBIF), and because there were large overlaps in the deviance which could be explained by sampling effort and the other predictors. The strong influence of sampling effort (sources) is evident when comparing z values: phylogenetic isolation z = -2.99 to -3.06; range size z = 2.70 to 5.54, native status (neophyte/archaeophyte) z = -3.06 to -4.14; log(sources) z = 44.70 to 69.62. After accounting for sampling effort (see Methods), the deviance explained by geographic range size, phylogenetic isolation and/or host plant native status ranged from a minimum of D = 0.007 – 0.025 (assuming that all shared deviance was explained by sampling effort) to a maximum of D = 0.758 – 0.830 (assuming that all shared deviance was explained by the predictor variables of interest).

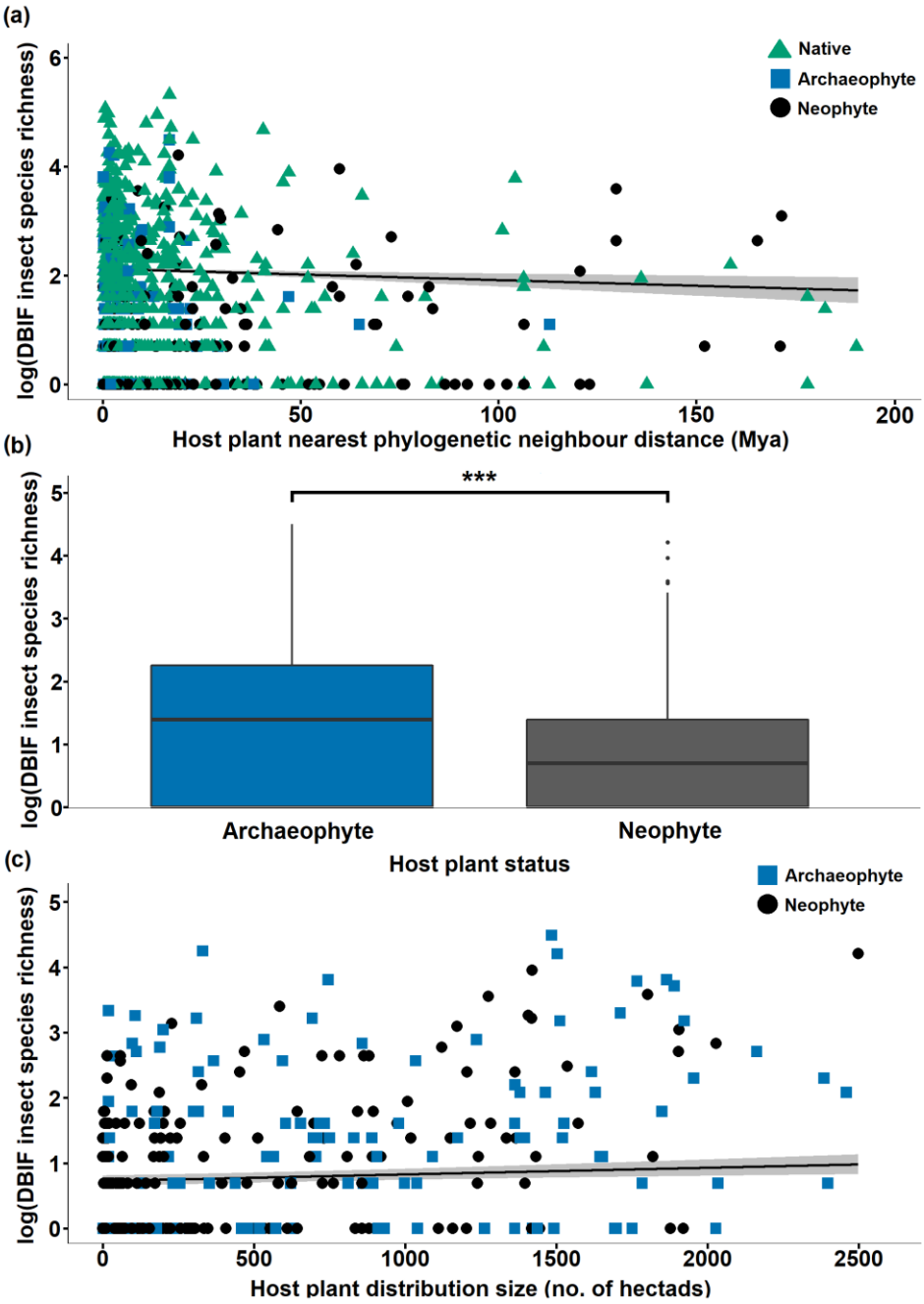


Figure 3.4: The effect of host plant phylogenetic isolation, native status, and range size on geographic-scale DBIF insect species richness. Partial regression plots (a) and (c) display the effect of our focal predictors (phylogenetic isolation and range size), whilst holding all other predictors at their mean. Shaded areas represent 95% confidence intervals. Data points represent individual plants species. Boxplots (b) represent median, interquartile range, and 1.5x the interquartile range. Boxplot points represent outliers. *** = significance of Tukey post-hoc contrasts < 0.001. Nearest phylogenetic neighbour distance (NPN) = distance in millions of years from host plant to closest phylogenetic neighbour in the DBIF. See Methods for details of the calculation of D^2 and D.

a) Negative binomial model (Richness ~ log(Sources) + NPN + Hectads) n = 1022, p (NPN) = 0.002, D^2 = 0.924, D = 0.010 – 0.829. **b)** Poisson model (Richness ~ log(Sources) + Status + Hectads) n = 352, p (Status) < 1e-04, D^2 = 0.927, D = 0.025 – 0.763. c) Negative binomial model (Richness ~ log(Sources) + Status + Hectads**)** n = 352, p (Hectads) = 0.002, D^2 = 0.927, D = 0.025 – 0.763.

3.4.4 Specialisation and community distinctiveness: Local-scale

Pollinator taxa were relative generalists, and were associated with a higher proportion of available plant species compared to the more specialised Vortis-sampled insect groups (d' specialisation index values: mean Vortis d' = 0.41 vs. mean pollinator d' = 0.26; Wilcoxon signed rank test: W = 1131, n of pollinators = 54, n of Vortis = 100, p < 1e-04). Consequently, a higher proportion of pollinator taxa (46%) were shared between plants of the three native status than was the case for the Vortis samples (26%) (**Fig. 3.5a; Fig. A2.7**). Recall that the abundance and richness of Vortis insects were predicted by phylogenetic isolation from the most closely related plant, whereas pollinators were also influenced by phylogenetic isolation from all other plants in the experimental plots (**Fig. 3.2; Tables A3.4 & A3.5**; **Fig. A2.5**). Thus, specialised insect faunas may be acquired primarily from similar, closely related sources, whereas the abundances and richness of generalists may depend on the wider plant community.

Exotic plants and congeners supported significantly more distinctive pollinator and Vortis communities than natives (**Fig. 3.5c; Fig. A2.8; Table A2.7**). Interestingly, 32% of Vortis insects (31 taxa) were only sampled from the non-native plants: either congeners or southern hemisphere exotics (**Fig. 3.5a**). The vast majority of these insects were British natives, and they represented a variety of taxonomic and functional groups, such as the omnivorous Mirid bug *Macrolophus rubi*, the herbivorous Delphacid bug *Megamelodes quadrimaculatus,* the herbivorous Lygaeid bug *Stygnocoris sabulosus*, and the detritivorous Throscid beetle *Trixagus dermestoides*. In contrast, only 9% (5 taxa) of the more generalised pollinators were uniquely sampled from non-native plants (**Fig. A2.7**). These were primarily native Lepidopteran species (Callophrys rubi, Tyria jacobaeae, Anthocharis cardamines, and Thymelicus sylvestris), although an unidentified Lacewing species was also uniquely present on non-native plants.

The presence of species uniquely sampled from non-native plants likely explains why a mixed community (composed of all the plants on the plots) accumulated richness at a rate comparable to that of a community of native plants alone (rarefaction analysis - **Fig. 3.3a, 3.3b**), despite the higher average richness of individual native plant species.

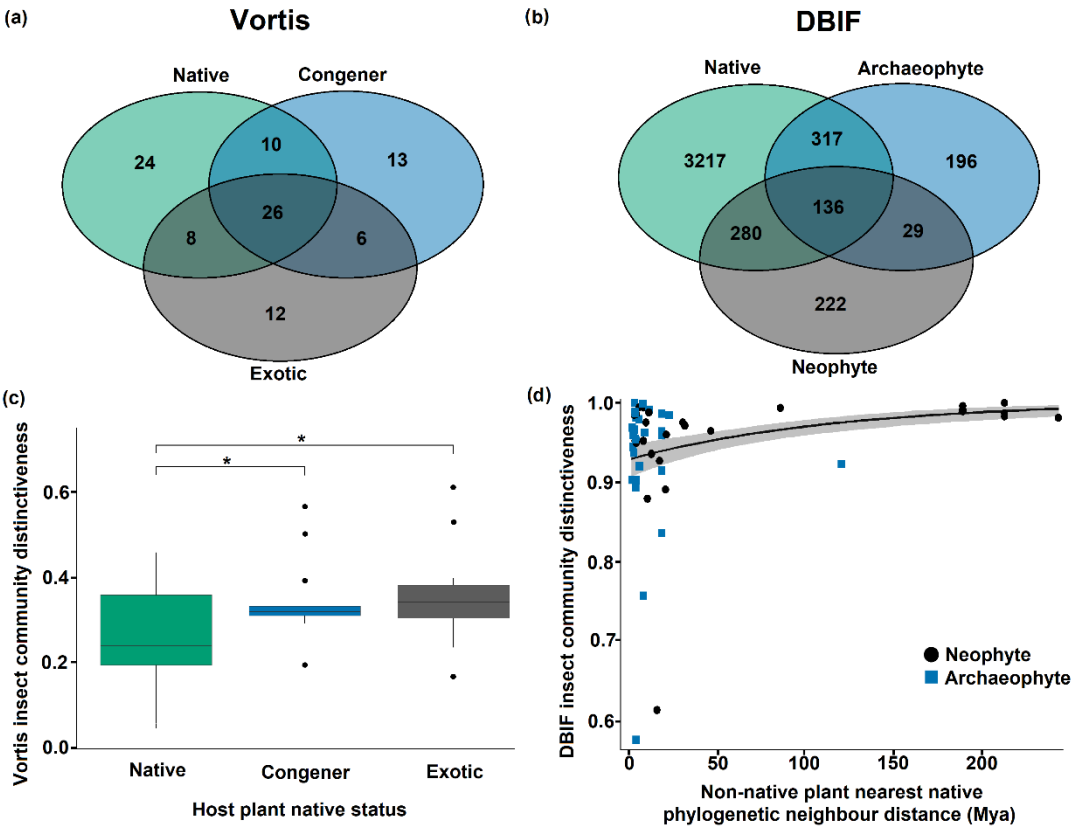


Figure 3.5: The effect of host plant native status and phylogenetic isolation on insect community distinctiveness. Distinctiveness was bounded between 0 and 1. See Methods for details of the calculation of pseudo R^2, and for the distinction between beta regression mean and precision submodels.

a) Venn diagrams displaying the number of local-scale Vortis taxa unique to, and shared between each host plant native status. Sample size of native = 14 plant species, congener = 13, exotic = 15. **b)** Venn diagrams displaying the number of geographic-scale DBIF species unique to, and shared between each host plant native status. Sample size of native = 679 plant species, archaeophyte = 120, neophyte = 234. **c)** Local-scale Vortis insect community distinctiveness on the different host plant statuses. Vortis insect distinctiveness was calculated using a non-metric multidimensional scaling approach (see Methods). Boxplots represent median, interquartile range, and 1.5x the interquartile range. Boxplot points represent outliers. * = significance of Tukey post-hoc contrasts < 0.05. Beta model (Vortis Insect Community Distinctiveness ~ Status) pseudo R^2 = 0.182. Sample size of native = 14 plant species, congener = 13, exotic = 15. **d)** Geographic-scale DBIF insect community distinctiveness with increasing host plant phylogenetic isolation. A partial regression plot displays the effect of our focal predictor (phylogenetic isolation), whilst holding all other predictors at their mean. Shaded areas represent 95% confidence intervals. Data points represent individual plant species. Non-native host plant nearest native phylogenetic neighbour distance (NPNN) = distance in millions of years from *non-native* host plant to closest *native* phylogenetic neighbour in the DBIF. The distinctiveness of the insect community on a plant was represented by dissimilarity from the pool of insects found on native plants (see Methods). Beta model (DBIF Insect Community Distinctiveness ~ log(Sources) + NPNN | NPNN) n = 56, p(NPNN) <1e-04, pseudo R^2 = 0.218.

3.4.5 Community distinctiveness: Geographic-scale

Non-native plants that were phylogenetically isolated from native plants supported the most distinctive insect communities (**Fig. 3.5d; Fig. A2.9; Table A2.8**). This was a highly significant and moderately sized positive effect (phylogenetic isolation z = 5.05 to 7.51, log(sources) z = -2.67 to -3.02). There were no significant effects of range size (number of hectads in Great Britain), neophyte versus archaeophyte status, or neophyte arrival date on insect community distinctiveness (**Table A2.8**).

Around 10% of DBIF insect taxa were only sampled from non-native plants: either archaeophytes or neophytes (**Fig. 3.5c**). The presence of species unique to non-native plants can be clearly seen in the sample-based rarefaction of the DBIF data, where a modelled mixed landscape of 1/3 natives, 1/3 archaeophytes, and 1/3 neophytes would be expected to host a comparable number of species at the reference sample size (2,073) to a landscape composed purely of natives (**Fig. 3.3c**), despite archaeophytes and neophytes accumulating insect species at a slower rate than natives.

3.5 Discussion

Together, the results indicate that novel plant habitats that share some similarities with long-standing 'native' plant habitats accumulate higher abundances and diversities of associated insect species compared with novel plant habitats that are more distinct. In this regard, plant origin (native, congener non-native, and exotic) and phylogenetic isolation are alternative proxies for the distinctive phenotypes of introduced plants that determine their suitability as habitats for insects, following their arrival in a new location. Thus, the results all point towards introduced plants accumulating more abundant and more diverse (species/taxon rich) communities of insects when they share some attributes (congeneric, low phylogenetic isolation; and hence an increased likelihood of chemical, nutritional and structural similarities) with long-standing native plants, compared with novel plants that are more distinct. Additionally, the highly significant positive effect of host plant range size on DBIF richness indicates that it is not only the "novelty" of a novel plant habitat that is important, but also its areal extent. The species-area effect is well established (Strong et al. 1977; Kenendy & Southwood 1984; Lawton et al. 1993; Andow & Imura 1994; Brändle

& Brandl 2001; Branco et al. 2015), but it is rarely considered alongside the effect of phylogenetic isolation. Our results suggest that phylogenetic isolation (expressed as phenotypic divergence) and range size work in tandem to influence the accumulation of richness in novel plant habitats.

It is important to acknowledge that variation in recording effort (measured as log(sources)) in the geographic-scale DBIF data had the strongest effect on measured species richness, compared to the nonetheless significant effects of host plant phylogenetic isolation, range size, and native status. This is a consequence of the large variation in the number of sources reporting data for insects associated with different plant species, combined with the well-established positive relationship between species richness and recording effort (e.g. Fisher et al. 1943). We call for more systematic and controlled sampling to be carried out at these broader geographic-scales. Despite this 'noise' in the DBIF database, the significant effects of phylogenetic isolation at a geographic-scale are consistent with the conclusions of the tightly controlled, local-scale experimental plots.

Analyses that considered time since introduction revealed that archaeophytes (pre-1500 arrivals) were more species-rich than neophytes (post-1500 arrivals), indicating species accumulation through time, at least on longer time scales. This is congruent with the conclusions of others in which richness can be observed to increase through time in novel plant and other habitats (both on geological timescales e.g. the last glacial maximum to present day, and successional timescales e.g. a century following forest clearing for agriculture – Kennedy & Southwood 1984; Nichols & Nichols 2003; Cramer et al. 2008; Brändle et al. 2008; Li et al. 2014). The specific date of introduction was not significant for the analysis of neophytes in the DBIF data, although the lack of an effect of time on shorter time scales (e.g. Kirichenko & Kenis 2016) may partly stem from the activity of entomological recorders, which has generally increased over time.

Vortis sampled insects were more specialised than pollinators. These results are consistent with insect pollinators being typically more generalised than other insect herbivores (Fontaine et al. 2009), and with British pollinators being particularly generalised when compared with pollinators from other regions (Blüthgen et al. 2006). Importantly, the accumulation of the more specialised Vortis insects on host plants was solely influenced by *nearest* phylogenetic neighbour/native neighbour distance, whereas the more generalised

pollinators were influenced both by *mean* phylogenetic isolation/isolation from natives, and *nearest* phylogenetic neighbour/native neighbour distance (richness models only). These results indicate that the characteristics of potential insect colonists may also influence colonisation. Specialised insect colonists may be primarily sourced from the single most similar habitat, whereas generalists may be recruited onto novel plant habitats from a wider range of sources.

Several lines of evidence indicate that some non-native plants play host to a unique and distinctive fauna: some insect species/taxa were uniquely sampled from non-native plants (9% of pollinators, 32% of Vortis insects, and 10% of DBIF insects; **Fig. 3.5**), exotic plants from the southern hemisphere supported significantly more distinct insect communities (for both pollinator and Vortis samples), phylogenetically isolated non-native plants supported the most distinctive insect communities (for DBIF data), and the species/taxon richness of insects in landscapes containing a mixture of native and non-native plants was high (sample-based accumulation curves). The 9% to 32% unique insect taxa on non-native plants is considerably higher than the 1-3% of insect taxa in the databases that are themselves non-native species (2% in the DBIF, 3% in the Wisley pollinator samples, and 1% in the Wisley Vortis samples; percentages based on the taxa identified to species level and of known historic status), meaning that the distinctive communities on non-native/phylogenetically isolated plants were primarily formed from the re-distribution of rare native insect species, rather than through the establishment of non-natives in new regions.

We recognise that additional sampling would be beneficial to establish the full host range of every insect in our datasets, but our results appear to contradict the suggestion that non-native plants solely host a small subset of the assemblages found on native plants (Perre et al. 2011). This is reminiscent of the way in which several human-altered habitats (e.g. brownfield sites, mine tailings, and green rooves) sometimes contain species that are rare or absent elsewhere (Eyre et al. 2003; MacIvor & Lundholm 2011; Jones & Leather 2012; Tischew et al. 2014**)**, and thus contribute to regional diversity. While the abundances and taxonomic richness of insects associated with novel plant habitats may be reduced at a local level, novel plant habitats may recruit taxa rarely found in native plant habitats, thus contributing to and potentially maintaining regional diversity. In our local-scale samples, taxon richness accumulation curves that pooled data for natives, congeners and

exotics were not significantly different to the curves for native-only or congener-only plants. Similarly, DBIF species richness accumulation curves that pooled data for natives, archaeophytes, and neophytes revealed that mixed landscapes accumulated richness at a similar rate compared with native only long-standing landscapes. We cannot conclude that the colonisation of novel plant habitats by unique taxa will increase overall regional diversity (e.g. Sax & Gaines 2003; Hiley et al. 2016; Vellend et al. 2017), but our results imply that a mixture of longer-standing and more novel plant habitats may retain diversity, albeit with a changed composition.

Under our framework, we hypothesise that non-native plants may function as analogues of novel anthropogenic habitats, and that understanding more about the processes underlying insect accumulation on non-native plants may provide some useful insights into the accumulation of species in novel anthropogenic habitats in general. Whilst we acknowledge that there may be difficulties in mirroring all aspects of novel habitat traits within plant biology, we suggest that there are parallels between introduced plants and other novel habitats. The sometimes divergent structures of non-native plants (e.g. plant height and branching complexity) and their associated microclimates may relate to the physical diversity of other novel habitats (be they mine tailings or urban heat islands), and non-native plants also contain an array of chemicals present in their tissues, exudates and associated soils, analogous to the chemical and soil diversity of post-industrial sites. We propose that host plant phylogenetic isolation may capture some of the aforementioned traits with a single metric, by operating as a proxy for the habitat novelty provided by differing host plant phenotypes. Further research is necessary to develop the frameworks required to quantify the relative “novelty” provided by other types of anthropogenic habitats (e.g. comparing green rooves versus biologically invaded communities), but time since non-native plant introduction and non-native plant range size represent the age and area (extent) of a novel habitat. Non-native plants represent one of the most numerous novel habitat types globally (Van Kleunen 2015), and are playing an increasingly prominent ecological role in virtually all landscapes (Schlaepfer et al. 2011). Thus, whilst our model system may not perfectly translate to other novel habitat types, novel plant habitats are certainly abundant, highly replicated, and important ecologically, making them an ideal model system to study.

To conclude, the similarity of a novel plant habitat to long-standing habitats can have a large impact on biological recruitment, affecting the abundances, richness and distinctiveness of the associated biota. Given the influence of phylogenetic position on host plant phenotypic traits (Schoonhoven et al. 2005; Cappuccino & Arnason 2006; Rasmann & Agrawal 2011; Bezemer et al. 2014), congener non-natives and species with low phylogenetic isolation were more likely to match natives in a variety of traits that determine how insects consume or otherwise associate with plants. We conclude that:

i) Novel plant habitats that are particularly divergent compared with existing habitats will initially be colonised by fewer taxa and individuals, although these colonists may be particularly distinctive.

ii) Novel plant habitats that occupy a larger area will be colonised by more species.

iii) Species richness in novel plant habitats will increase over time (plant arrival before vs. after 1500), although the schedule of accumulation on shorter timespans remains uncertain.

iv) The 'novelty' of a novel plant habitat should be viewed in relation to the attributes of potential colonists. More generalised colonists may respond to the structural, chemical and ecological differences between a novel plant habitat and a wide array of existing habitats, whereas more specialised colonists may be primarily influenced by the differences between the novel plant habitat and a much smaller subset of similar existing habitats.

v) The faunal richness of regions that contain relatively even mixtures of long-standing and novel plant habitats will be similar to that found in regions with just long-standing habitats, due to the colonisation of novel plant habitats by unusual taxa.

Overall, the more divergent a novel plant habitat is from existing habitats, the lower the total abundance of associated insects and the less local α-diversity that it will attract (at least initially). However, the higher distinctiveness of its biota may contribute to regional richness.

3.6 Acknowledgements

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Chapter 4 The development of Anthropocene biotas: colonisation of novel plant habitats by native and non-native insects

The native Burnet moth (Zygaena filipendulae) on non-native Argentinian vervain (Verbena bonariensis)

4.1 Abstract

The movement of species into new regions is a defining feature of the Anthropocene, and is often facilitated by the creation of novel anthropogenic habitats. However, uncertainty remains over the relative use of novel habitats by native and non-native species (species perspective of 'habitat'), and their combined influence on coarser-scale species accumulation in more or less novel ecosystems (land use or ecosystem-level perspective). Here, I consider non-native plants in Great Britain as novel habitats from the perspective of insect colonists (species perspective), set within ecosystem types that are relatively more (gardens) or less (the wider countryside) novel. I analyse geographic-scale data contained within two extensive datasets (the Database of Insects and their Food Plants, and the Royal Horticultural Society Entomology Advisory Database), which together capture native and non-native insect associations with native and non-native plants in gardens and in the wider countryside. Analyses reveal that novel interactions are widespread, with large numbers of native insects found on non-native plants (37% of records across both datasets). Non-native insects in novel garden ecosystems are almost exclusively associated with non-native plants, and these plants are more distinctive (based upon phylogenetic distance from native plants) than those colonised by native insects. Most native insect species are also associated with non-native plants within gardens (reflecting the preponderance of non-native plants in these ecosystems), but not in the wider countryside, where most native insects are recorded on native plants. Interestingly, non-native plants in both gardens and the wider countryside often support native insect species that are rare on native plants, suggesting a role for non-native elements of ecosystems in the maintenance of native insect biodiversity. Overall, these results reveal the widespread integration of native and non-native biotas, although there are different proportions of interactions among species of different origins.

4.2 Introduction

The creation of novel habitats and the accumulation of unusual species mixtures within them continue to form novel ecosystems as the Anthropocene progresses (Hobbs et al. 2006, 2009; Radeloff et al. 2015; Evers et al. 2018; Padovani et al. 2019). The movement of species into increasingly-modified ecosystems may explain why biodiversity has remained relatively stable locally (through the balance of gains and losses), and has typically increased at the regional scale (through colonisation of novel habitats exceeding losses from remaining historic ones), despite global declines (Sax & Gaines 2003; Loh et al. 2005; Thomas 2013a,b; Vellend et al. 2013; Dornelas et al. 2014; Thomas 2015; Vellend et al. 2017; Dornelas et al. 2019). Understanding biodiversity change requires us to evaluate the ecological and evolutionary causes of and limits to species accumulation in novel habitats, in terms of both biological interactions (e.g. herbivorous insects feeding on non-native plants) and larger-scale associations in the novel ecosystems that house those interactions. Novel habitats typically host a greater proportion of non-native species than is found in pre-existing ecosystems (McKinney 2002; Lugo & Helmer 2003; Bonter et al. 2010). However, uncertainty remains regarding the development of novel interactions and habitat associations within new biological assemblages.

Here, novelty is defined in two ways. Non-native plants represent novel habitats from the perspective of (native) plant-associated insect species (Padovani et al. 2020), and hence I refer to these as 'novel plant habitats'. I categorise habitat age as long-standing for native plants, intermediate for non-native archaeophytes (plants introduced to Great Britain by 1500) and recent for neophyte plant species (arrival in Great Britain since 1500). Additionally, I capture the differences between novel plant habitats by quantifying their phylogenetic distinctiveness from the native flora. Host plant phylogeny is a convenient proxy for habitat "novelty" from the perspective of plant-associated insects (Padovani et al. 2020) as it influences an array of plant phenotypic traits (e.g. phenology, toxic secondary plant compounds, olfactory attractants, and physical structure - Schoonhoven et al. 2005; Cappuccino & Arnason 2006; Rasmann & Agrawal 2011; Bezemer et al. 2014), and so affects the composition and diversity of insect faunas (Grandez-Rios et al. 2015).

I also consider novelty at a 'higher level', in which ecosystems (or land use classes) differ in their degree of novelty. This study distinguishes between novel garden ecosystems (in

which non-native plants are typically in the majority - Loram et al. 2008) and the wider landscape i.e. less novel ecosystems (where native plant species are usually predominant - Thomas & Palmer 2015). Thus, my analyses provide both species-habitat and ecosystem-level perspectives of the development of novel interactions.

I analyse more than 100 years of British insect records contained within two geographic-scale databases, reporting the interactions of herbivorous insects (and mites) with plants in gardens (RHS Entomology Advisory Database; RHS) and in the wider landscape (Database of Insects and their Food Plants; DBIF). With these data, I quantify the extent to which non-native insect species disproportionately associate with novel plant habitats within novel ecosystems (gardens). Additionally, I contrast the novel plant habitat associations of native insects within more or less novel ecosystem types (gardens vs. the wider countryside). Elucidating the mechanisms underpinning the accumulation of non-native species within pre-existing and novel habitats/ecosystems is particularly important as there is no clear indication of saturation in non-native species accumulation worldwide (Seebens et al. 2017). Non-native species are predicted to be increasingly important for the provision of ecosystem services in future (Williams 1997; Ewel & Putz 2004; Tassin & Kull 2015), although invasive non-natives may have a range of negative economic and ecological impacts (McGeoch et al. 2010). Understanding how native species accumulate in novel habitats/ecosystems is also important, as there indications that novel habitats may have a role to play in the maintenance of native species diversity (Eversham et al. 1996; Kowarik 2011; Moroń et al. 2014; Padovani et al. 2020).

Globally, insects represent the majority of animal species which have established populations outside of their native ranges (Roques 2010; Seebens et al. 2017). Whilst most non-native insects in Great Britain do not pose a threat to the economy or to native biodiversity (Roy et al. 2012; Smith et al. 2018), the rate of introductions is increasing (Smith et al. 2018), in common with many other parts of the world (Seebens et al. 2017). Non-native insects are becoming an increasingly prominent feature of the British fauna, but there is little information on their accumulation in both pre-existing and anthropogenic novel habitats. Whilst the mechanisms determining the spread of certain non-native insects of ecological or economical concern have been well studied (e.g. the Horse Chestnut leaf miner *Cameraria ohridella* – Gilbert et al. 2004; the harlequin ladybird *Harmonia axyridis* – Roy & Wajnberg 2008; the Lily beetle *Lilioceris lilii* – Salisbury 2008),

few have contrasted the habitat associations of entire native and non-native insect assemblages. Most insect introductions to Great Britain and mainland Europe are associated with the ornamental plant trade (Kenis et al. 2007; Smith et al. 2007; Liebhold et al. 2012), and non-native insects may be more reliant on non-native plants than native insects (Kenis et al. 2007; Rodríguez et al. 2019). However, the phylogenetic, temporal, and spatial mechanisms that determine these associations are uncertain; i.e., how does the distinctiveness and duration that a non-native plant has been present, and the novelty of the ecosystem that it grows in, affect the accumulation of associated non-native species?

A further potential dimension of the novelty of associations is the geographical origin of introduced insects, and hence I also consider this variable. I also test insect specialism as a possible determinant of the colonisation of plant species by native and non-native insects (Brändle et al. 2008; Spafford et al. 2013; Grandez-Rios et al. 2015; Rodríguez et al. 2019). I summarise the total proportions of novel interactions found across both datasets, and test (i) whether non-native insects in novel garden ecosystems are significantly more associated with novel (non-native) plant habitats than native insects, and (ii) if ecosystem type (highly modified gardens - RHS vs. more natural/semi-natural landscapes – DBIF) influences the associations of native insects with novel plant habitats. Additionally, I test (iii) whether insect status (native, non-native), specialism or geographical origin are associated with the "novelty" (i.e. phylogenetic isolation) of novel plant habitats, and (iv) if insect status or specialism are related to novel plant habitat age (native vs. archaeophyte vs. neophyte plants). I also test (v) whether unique native insect communities accumulate on novel plant habitats in both the wider countryside and in novel garden ecosystems, thus (vi) increasing or maintaining native insect diversity in areas of mixed habitat types (pre-existing native vs. novel).

4.3 Materials and Methods

4.3.1 The Royal Horticultural Society Entomology Advisory Database (RHS)

The Royal Horticultural Society Entomology Advisory Database (RHS) details 78,420 interactions between invertebrates and garden plants recorded in Great Britain (and

Northern Ireland – 236 records) from 1905 to 2018. The RHS Entomology Advisory service is available to all RHS members free of charge, and facilitates the identification of invertebrate specimens found within their gardens. Interaction data were submitted by RHS members to the Entomology Advisory team, who identified specimens, relayed the information back to members, and recorded the interaction within the database. Invertebrate taxa were identified to as close to species level as possible, whilst plant taxonomic level depended on the information provided by the RHS member. Interactions represent insect species *x* associated with host plant *y* and do not include abundance information.

4.3.2 The Database of Insects and their Food Plants (DBIF)

The Database of Insect and their Food Plants (DBIF – Ward 1988; Smith & Roy 2008; Ward et al. 2019) reports 60,222 interactions between insect (and mite) species and plants recorded primarily in the wild in Great Britain and Europe from 1891 to 2009. Interactions are reported from a wide variety of sources, including field guides (e.g. Heath & Emmet 1979) and entomological journals (e.g. The Entomologists Gazette). Interactions represent insect species *x* associated with host plant *y* and do not include abundance information.

4.3.3 Database cleaning

Only 'higher' plants (seed plants and ferns) were analysed, and I excluded certain invertebrate groups from the RHS (Diplopoda, Collembola, Mollusca, Nematoda, and Symphyla) because of low taxonomic resolution and/or because they were not included in the DBIF. I excluded insect-plant records of uncertain British origin from the DBIF, and excluded data from captive breeding studies. I also excluded DBIF records that had not been expertly verified by L. K. Ward, and thus included in previous large-scale analyses (e.g. Ward 1988; Ward & Spalding 1993; Ward et al. 1995; Ward et al. 2003; Padovani et al. 2019). Only invertebrate (insects and mites, hereafter referred to as 'insects') and plant records at a species level resolution were included. All sub-species/cultivars/varieties were "upgraded" to the species level. UKSI (United Kingdom Species Inventory) codes, Stace's "New Flora of the British Isles" (2010), Kew Plants of the World Online (2019), the Fauna Europaea (de Jong et al. 2014), and the EPPO Global Database (2019) were used to group together plant and insect species listed under different synonyms. Within the trimmed RHS dataset, 2,193 out of 9,334 records were of uncertain geographic origin, but the vast

majority will have originated in Great Britain (RHS membership statistics June 2019: GB = 97.41%, Northern Ireland = 0.19%, overseas = 2.40%).

4.3.4 Host plant native status assignment

Plant native status was assigned from several sources. Archaeophyte (non-native, arrived before 1500), and established neophyte (non-native, arrived since 1500, recorded outside of horticultural settings) statuses were sourced from Stace & Crawley's "Alien Plants" (2015). PlantAtt (Attributes of British and Irish Plants – Hill et al. 2004) was used to identify which plants were native, with Stace's "New Flora of the British Isles" (2010) confirming 15 additional DBIF native plants that were either not included in PlantAtt, or were listed with an uncertain status.

Any remaining unclassified plants within the RHS Entomology Advisory database were investigated further using Kew Plants of the World Online (2019). Two additional plant native status categories were assigned using the native ranges of these missing plants. Plants arriving from the New World or outside of the North African/European zone (east of the Ural Mountains) were highly unlikely to have arrived in Great Britain prior to 1500, and so were classified as garden neophytes. These garden neophytes represent non-native plants unique to gardens and not present in the wild as naturalised or casual plants, and hence they are not listed in Stace & Crawley (2015). Plants originating from the North African/European (west of the Urals) zone were designated as 'uncertain status', as it was not possible to determine whether they had arrived before or after 1500. These uncertain status plants were excluded from any analyses that involved the comparison of archaeophytes and neophytes. Additionally, 53 interspecific hybrids were excluded from the analysis of the RHS database. The final RHS dataset consisted of 100 native plant species, 30 archaeophytes, 165 established neophytes, 299 garden neophytes, and 59 uncertain status non-natives.

Garden neophytes within the DBIF were left unclassified so that the DBIF analysis would better represent the diversity of British insects in the wider countryside. Overall, 76 plant species could not be classified as native, archaeophyte, or established neophyte, and so were excluded from the analysis of the DBIF dataset. Also excluded were 19 hybrids. The final DBIF dataset considered here consisted of 669 native plant species, 119 archaeophytes, and 214 neophytes.

4.3.5 Insect native status, origin and functional group assignment

Insect non-native status was assigned using the Great Britain Non-native Species Information Portal (NNSS 2019). As there is no definitive list of all British native insects, I removed all non-native insects from the UKSI (United Kingdom Species Inventory), and then used the remainder of the UKSI to assign native status to the insect species within both datasets. Insect histories are less well known than those for plants, (and hence some historic introductions may be classified as 'native' species), but non-native insect species have clearly been established in Great Britain for shorter periods than those classified as native.

228 DBIF and 91 RHS insect species were of uncertain native status, and so were excluded from all analyses. All records within the DBIF dataset reported insect functional group, aside from 13 records that were excluded. The final DBIF data set consisted of 12,719 interactions between plants and 4,054 native herbivores, 37 native omnivores, and 75 non-native herbivores. RHS insect feeding type was assigned using the interactions reported within the DBIF, and via a literature search for any insects not found in the DBIF (111 species). 63 records were excluded as they involved garden insects that were predators, parasitoids, detritivores, broad generalist scavengers, or of uncertain functional group. The final RHS dataset consisted of 9,334 interactions between garden plants and 379 native herbivores, 2 native omnivores, and 53 non-native herbivore species.

I also determined the geographic origin of all RHS non-native insects in order to test for any possible influence of origin on associated plant habitat novelty (phylogenetic isolation). Insect geographic origins were obtained from the Great Britain Non-native Species Information Portal (NNSS 2019), and via an additional literature search for six uncertain cases. Our origin categories were: Afrotropical (1 insect species), Asia (12), Australasia (6), Europe/North Africa (17), New World (10), and Cosmopolitan (1). Five insect species occurred in Europe/North Africa and in one or more other categories (but were not cosmopolitan). These insects were classified as Europe/North Africa, presuming that species were relatively likely to arrive from closer parts of their ranges. See **Table A3.1** for the geographic origin of each non-native insect species.

4.3.6 Host plant phylogenetic relationships

Phylogenetic relationships between plants were obtained from a global phylogeny of vascular plants (Qian & Jin 2016), and the R package pez (Pearse et al. 2015) was used to produce a phylogeny that included the entire native British flora (as determined from PlantAtt – Hill et al. 2004), and the non-native plants found within the two databases. Where plant species were not found in Qian & Jin's megaphylogeny (25% of species) all members of their clade were replaced with a polytomy. Three RHS and one DBIF non-native plant species could not be assigned a place in the phylogeny as they were from clades not found in Qian & Jin's megaphylogeny, and so they were excluded from analyses of host plant phylogenetic isolation. I chose to focus on the phylogenetic isolation of non-native plants only as the sample size of RHS non-native insects on native plants was very small (29 records). Two measures of phylogenetic isolation were calculated for each non-native plant:

1) Mean phylogenetic isolation from natives: The mean divergence time (in millions of years) from a non-native plant species to all native British plant species.

2) Nearest native phylogenetic neighbour distance: The divergence time from a non-native plant species to its closest native British neighbour.

4.3.7 Statistical analysis

Given that the primary focus of the DBIF was on British insects (Ward 1988), non-native insects were severely under sampled (75 species, 171 records). These DBIF non-native insects were included in higher level summary statistics detailing the total number of novel interactions across the two datasets, but were excluded from all statistical analyses, and from the quantification of insect specialism as d'.

All statistical analyses were carried out in R (R Core Team 2018) using R Studio (RStudio Team 2016). See **Appendix 3A** for full a list of R packages used. I carried out analyses on both datasets, but differences between the RHS and DBIF data meant than on some occasions the analyses are comparable rather than identical (in extremis, possible for one data set, but not for the other); as detailed below.

Insect specialism was calculated with the d' index (Blüthgen et al. 2006). The number of times that an entity (insect or plant) interacted with all other available partners

(determined as the proportion of observed links out of those possible) was used when calculating d'. Therefore, d' is interpreted as the deviation of an insect's actual interaction frequencies from a null model which assumes that all plant partners were used in proportion to their availability. Possible d' values range from 0 (perfect generalist) to 1 (perfect specialist). DBIF and RHS datasets were treated separately when calculating d' because the insects and plants within each dataset were part of two different interaction webs, and experienced different sampling protocols and origins (garden ecosystems vs. the wider landscape). Thus, DBIF and RHS datasets were always analysed separately when including d' in the analyses.

The overall effect of insect native status on the number of interactions with plants of different native status (RHS and DBIF = native/archaeophyte/neophyte; RHS = native/archaeophyte/established neophyte/garden neophyte) was tested with χ^2 tests, with a Bonferroni correction employed for subsequent pairwise plant native status comparisons. Due to the potential influence of variation in recording effort across insect species I also tested proportional host plant use per insect. The proportion of native vs. non-native, archaeophyte vs. neophyte, and established neophyte vs. garden neophyte (RHS only) host plant records was calculated for each insect, and the effect of insect native status and/or specialism on plant use was tested with beta GLM regression (d' tested separately within the RHS and DBIF datasets – see above). The effect of novel habitat location (RHS = gardens, i.e. highly modified ecosystems; DBIF = the wider landscape, i.e. less modified ecosystems) on the plant use proportions of the 253 native insect species that were recorded in both the DBIF and RHS datasets was also tested with beta GLM regression. Prior to regression, host plant proportions were transformed to >0 and <1 via *(proportion − (sample size − 1) + 0.5)/sample size*, as beta regression cannot handle values of 0 and 1 (Smithson & Verkuilen 2006). All beta GLM models were specified with a log link. Good model fit was determined via inspection of diagnostic plots, and via calculation of pseudo R^2 values (the beta GLM equivalent of R^2 - McFadden 1973). Only beta GLM mean submodel test values are reported here: the beta GLM mean submodel reports the influence of regressors on the mean of a dependent variable, whereas the beta GLM precision submodel quantifies the effect of model regressors on dependent variable dispersion (Cribari-Neto & Zeileis 2010). Likelihood ratio tests determined the inclusion/exclusion of variables in beta GLM models.

The association of insect native status and RHS non-native insect origin with non-native host plant phylogenetic isolation were tested with Gamma GLMM and GLM regression specified with a log link, as both metrics of phylogenetic isolation were ≥ 0, and so did not fit a Gaussian distribution. Gamma GLMM analyses used penalized quasi-likelihood with insect genus as a random effect, thus accounting for the likely influence of insect taxonomy on host plant associations, and allowing sufficient remaining variation to detect an effect of insect native status (testing revealed that inclusion of insect species as a random effect masked any effect of insect native status). Only insect genera that interacted with non-native plants 10 or more times within each data subset (depending on inclusion of d' as a predictor – see above) were included in GLMM analyses, following standard practice for GLMM random effect sample sizes (Bolker et al. 2009). GLMM analyses tested the associations of insect native status or origin with the phylogenetic isolation of the host plants involved in each interaction, whereas GLM analyses tested the mean phylogenetic isolation of all host plants per insect. GLM analysis was employed so that all insects could be included (given the exclusion of under sampled genera during GLMM analysis). Good GLMM model fit was determined via inspection of diagnostic plots, and via calculation of marginal and conditional trigamma pseudo R^2 values. Marginal pseudo R^2 represents the proportion of variance uniquely explained by a fixed effect, whilst conditional pseudo R^2 represents the proportion of variance explained by both fixed and random effects (Nakagawa et al. 2017). Good GLM model fit was determined via inspection of diagnostic plots, and via calculation of D^2. D^2 is the GLM equivalent of R^2, and represents the proportion of deviance explained by a model (Guisan & Zimmermann 2000). Sampling effort was quantified as the number of unique data sources (DBIF = literature sources, RHS = enquiry reference numbers) and insect species combinations within each database, and was tested for inclusion in all Gamma GLM models. Likelihood ratio tests determined the inclusion/exclusion of variables in Gamma GLM models.

I used sample-based rarefaction (Colwell et al. 2012) to model the accumulation of native insect species richness on host plants of different native status within the two datasets separately. All plants within each status category (native, archaeophyte, and neophyte) were pooled, and rarefaction confidence intervals were estimated via bootstrapping 10,000 times. Within the DBIF data a rarefaction sample was classified as a unique data source (normally a single article or other publication) and plant species combination.

Within the RHS data a rarefaction sample was classified as a unique record number and plant species combination.

I also implemented a 'combined' rarefaction that displayed the accumulation of richness in a mixed community. This line equalised the number of sources from plants of different native status, and was composed of a summary of the rarefaction of 200 random samples consisting of 1/3 native, 1/3 archaeophyte, and 1/3 neophyte species, with each individual rarefaction bootstrapped 10,000 times. For the DBIF mixed line the upper bound was the *minimum* of the 200 upper 95% confidence intervals, and the lower bound was the *maximum* of the 200 lower 95% confidence intervals (thus demonstrating as conservatively as possible overlap between the mixed and native communities. For the RHS mixed line the upper bound was the *maximum* of the 200 upper 95% confidence intervals, and the lower bound was the *minimum* of the 200 lower 95% confidence intervals (thus demonstrating as conservatively as possible no overlap between the mixed and native communities). Non-native plants of uncertain neophyte/archaeophyte status were excluded from the RHS rarefaction analysis, and established and garden neophytes were grouped together.

4.4 Results

The RHS records contained 9,334 interactions between 381 native and 53 non-native insect (and mite) species, and 100 native plant species, 30 archaeophytes, 165 established neophytes, 299 garden neophytes, and 59 uncertain status non-natives. The DBIF records contained 12,719 interactions between 4,091 native and 75 non-native insect (and mite) species, and 669 native plant species, 119 archaeophytes, and 214 neophytes. RHS records were widely distributed across Great Britain (see **Fig. A3.1**; DBIF records did not contain precise locations). Insect species represented a variety of orders, with the five most abundant in the RHS data being Hemiptera (4,087 records; ~44%), Trombidiformes (2,015; 22%), Diptera (1,094; 12%), Lepidoptera (1,058; 11%), and Coleoptera (705; 8%), and the five most abundant in the DBIF data being Lepidoptera (6,839 records; 54%), Hemiptera (1,982; 16%), Diptera (1,749; 14%), Coleoptera (1,112; 9%), and Hymenoptera (514; 4%).

Of the 22,053 records in the combined RHS and DBIF datasets 48% of those represented novel interactions (i.e., at least one partner was a non-native species). Of those, most novel interactions consisted of native insects on non-native plants (78%, 8,233 records). 22% (2,283 records) represented non-native insects on non-native plants, and <1% (66 records) were of non-native insects on native plants.

4.4.1 Host plant native status

χ^2 tests demonstrated that native herbivorous insects were more strongly associated with non-native plants when these occurred in novel garden ecosystems compared with in the wider-countryside (**Fig. 4.1**; **Table A3.2**): 83% of records of native herbivorous insects in the wider countryside DBIF data were associated with native plants, compared with 17% of records in the garden RHS data. Non-native insects within gardens were even more strongly associated with non-native plants, and especially with plants that had been introduced since 1500 (neophytes; **Fig. 4.1**; **Table A3.2**): Only 1% of RHS garden records reported non-native insects on native plants, and 88% of non-native insect records were from neophytes (comparing native and non-native insects was only possible in the RHS data – see Methods).

Considering each insect species individually, beta GLMs revealed that most native insects (76%) interacted solely with native plants in the countryside (DBIF), whilst most native (54%) and non-native insects (76%) interacted solely with non-native plants in novel garden ecosystems (RHS) (**Fig. 4.2a; Table A3.3 – Model 1**). Additionally, I observed a significant shift towards non-native plants when contrasting native insect species in gardens with their conspecifics in the wider countryside (253 native insect species occurred in both ecosystem types; **Fig. 4.3a; Table A3.4 – Model 1**).

Similar trends exist for associations with plants that were introduced to Great Britain at different times. Native insects were often recorded on non-native plants that were introduced before 1500 (archaeophytes) in the countryside, whereas both native and non-native insects were predominantly recorded on plants introduced after 1500 (neophytes) in gardens (although native insects associated with more archaeophytes than non-natives **– Fig. 4.2b; Table A3.3 – Model 2**). Similarly, there was a significant shift towards neophyte plants when contrasting individual native insect species in gardens and the wider countryside (**Fig. 4.3b; Table A3.4 – Model 2**). Finally, within gardens native insects were

primarily associated with neophyte plant species that are also established in the wider countryside, whereas non-native insects were marginally ($p < 0.1$) more likely to associate with neophytes that are only maintained within gardens (**Fig. 4.2c; Table A3.3 – Model 7**).

Specialised native insects in the wider countryside (DBIF) were more strongly associated with non-native plants vs. natives, and neophytes vs. archaeophytes, although the variance explained by both models was very small (**Fig. A3.2; Table A3.3 – Models 3 & 4**). Specialised insects (both native and non-native) in novel garden ecosystems (RHS) were more associated with native plants vs. non-natives, neophytes vs. archaeophytes, and were particularly strongly associated with neophytes that are unique to gardens compared with those that also occur in the countryside (**Fig. A3.3; Table A3.3 – Models 5, 6 & 7**).

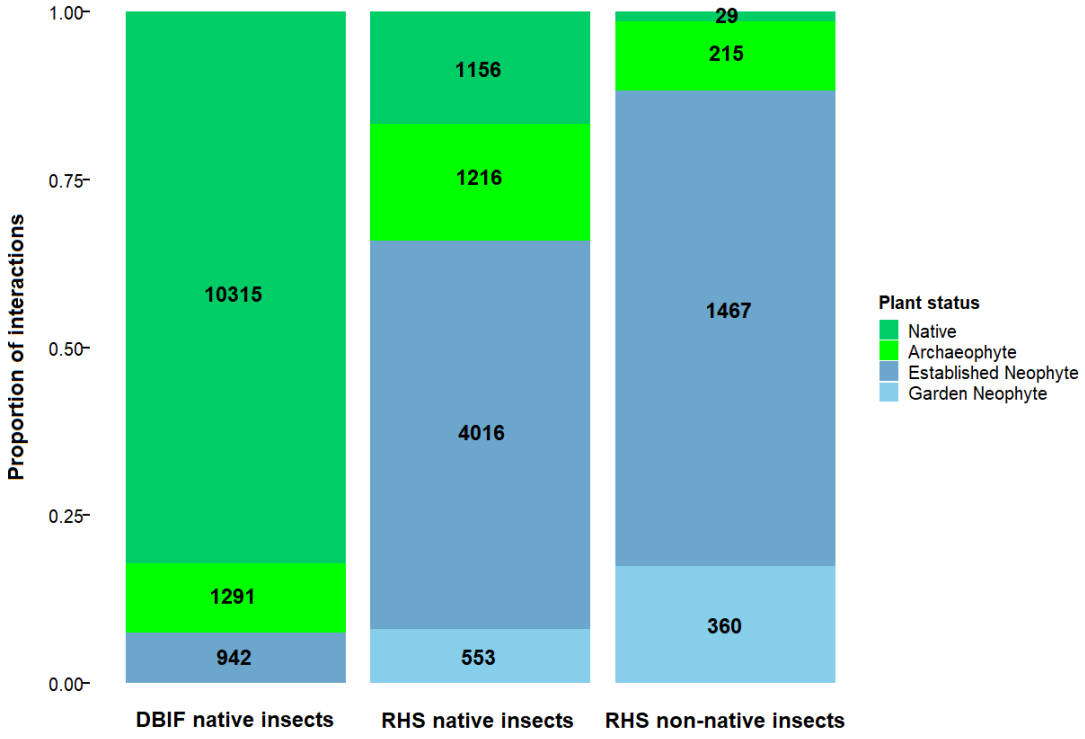

Figure 4.1: Interactions frequencies of DBIF native, RHS native and RHS non-native insects with different host plants. RHS insects were sampled in novel garden ecosystems, and DBIF insects were sampled in the wider landscape. Numbers on plots represent the number of interactions within each category. See Methods for details of host plant native status categories.

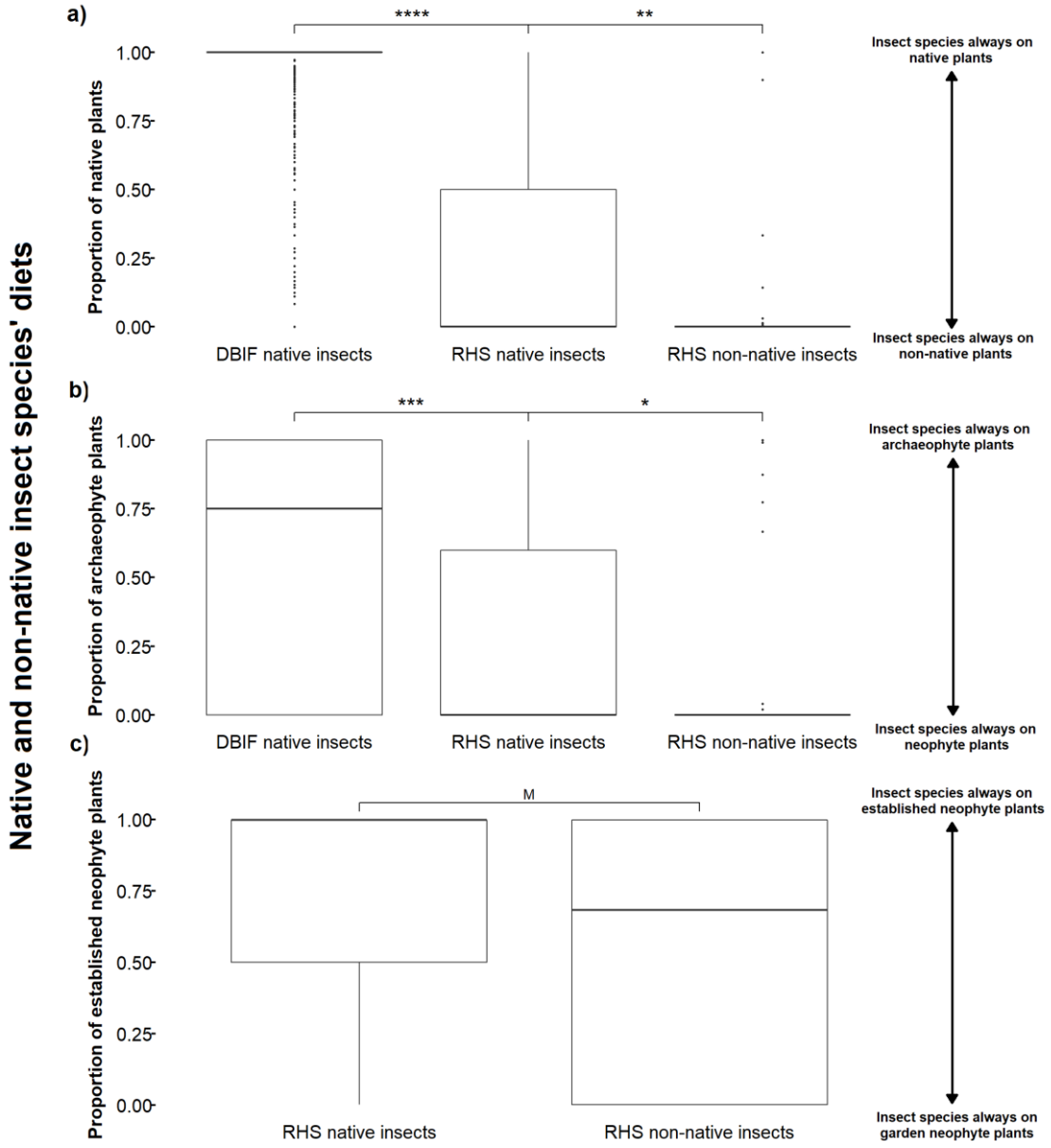

Figure 4.2: Associations of insect species with native and non-native plants. RHS insects were sampled in novel garden ecosystems, and DBIF insects were sampled in the wider landscape. Beta regression tested the effect of insect species' native status and/or ecosystem type on proportional use of different host plants. Boxplots represent median, interquartile range, and 1.5x the interquartile range. Points represent diet of outlier insect species. Significance of Tukey post-hoc contrasts M = marginal p <0.1, * <0.05, ** <0.01, *** <0.001, **** < 1e-04. Pseudo R^2 represents the proportion of variance explained by a model. d' = insect specialism. See Methods for details of host plant native status categories, the distinction between beta regression mean and precision submodels, and the calculation of d'.

a) beta GLM model (Records on Native Plants/Records on All Plants ~ Insect Native Status/Ecosystem Type | Insect Native Status/Ecosystem Type) pseudo R^2 = 0.224, number of DBIF native insect species = 4091, RHS natives = 364, RHS non-natives = 51.

b) beta GLM model (Records on Archaeophyte Plants/Records on All Non-Native Plants ~ Insect Native Status/Ecosystem Type | Insect Native Status/Ecosystem Type) psuedo R^2 = 0.088, number of DBIF native insect species = 994 insect species, RHS native = 297, RHS non-native = 48.

c) beta GLM model (Records on Established Neophyte Plants/Records on All Neophyte Plants ~ Insect Native Status + d' | d') psuedo R^2 = 0.145, number of RHS native insect species = 245, RHS non-natives = 43.

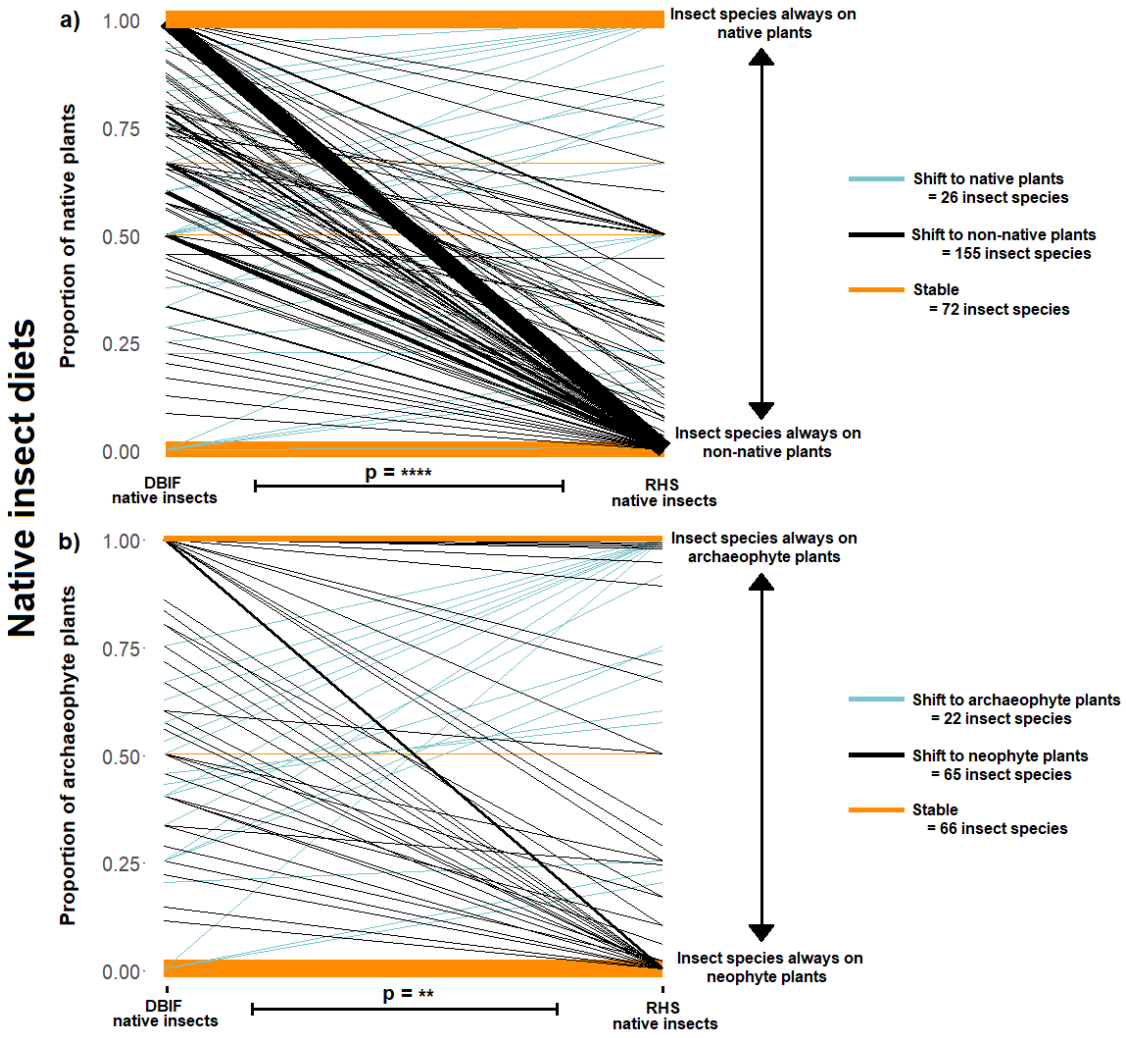

Figure 4.3: Associations of native insect species with native and non-native plants in different ecosystem types. RHS = novel garden ecosystems, DBIF = the wider landscape. Beta regression tested the effect of ecosystem type on the proportional use of different host plants by the native insect species that were sampled within both the RHS and the DBIF. Lines connect the host use of each insect species in the two ecosystems types. Line thickness represents the number of insect species with overlapping dietary shifts. Significance of contrasts ** = p <0.01, **** <1e-04. Pseudo R^2 represents the proportion of variance explained by a model. d' = insect specialism. See Methods for details of host plant native status categories, the distinction between beta regression mean and precision submodels, and the calculation of d'.

a) beta GLM model (Records on Native Plants/Records on All Plants ~ Ecosystem Type + Sampling Effort | Ecosystem Type*Sampling Effort) pseudo R^2 = 0.162, number of DBIF native insect species = 253, RHS natives = 253.

b) beta GLM model (Records on Archaeophyte Plants/Records on All Non-Native Plants ~ Ecosystem Type) psuedo R^2 = 0.033, number of DBIF native insect species = 153, RHS natives = 153.

4.4.2 Non-native host plant phylogenetic isolation

Gamma GLMs and GLMMs demonstrated that non-native insects in novel garden ecosystems (RHS) were associated with more phylogenetically isolated non-native plants than native insects (**Fig. 4.4, Table A3.5 – Models 1 & 2, Table A3.6 – Models 1 & 5**). The effect sizes attributed to insect native status were small (marginal pseudo R^2/D^2 ranged from 0.028 – 0.095), but overall GLMM model fit was high (conditional pseudo R^2 = 0.448 – 0.684; conditional pseudo R^2 included the variance explained by both insect native status as a fixed effect and insect genus as a random effect).

Gamma GLMs indicated that native insects in the wider countryside (DBIF) were associated with more phylogenetically-isolated non-native plants than native insects in gardens (RHS), although the effect size attributed to insect native status was extremely small (D^2 = 0.005; **Table A3.6 – Model 6**), and a similar result was not replicated in the equivalent Gamma GLMM model (**Table A3.5 – Model 3**).

There was some indication that native insect specialists in the wider countryside (DBIF) were associated with more phylogenetically isolated non-native plants than generalists. However, the effect sizes attributed to insect specialism (d') were very small (Gamma GLMM marginal pseudo R^2 ranged from 0.008-0.012; **Table A3.5 – Models 5 & 6**), and these results were not replicated in equivalent Gamma GLM models (**Table A3.6 – Models 8 & 9**). Both native and non-native insect specialists in gardens (RHS) were associated with more phylogenetically isolated non-native plants than generalists, although this effect was stronger for non-native insects (**Fig. A3.4; Table A3.6 – Models 1–4**).

Non-native insect origin was a significant predictor of host plant phylogenetic isolation in both Gamma GLMM models (**Table A3.7**). However, this effect likely emerged from uneven sampling of insects from different origins, as the effect was lost entirely when mean host plant phylogenetic isolation was tested for all insects (Gamma GLM method – **Table A3.8**).

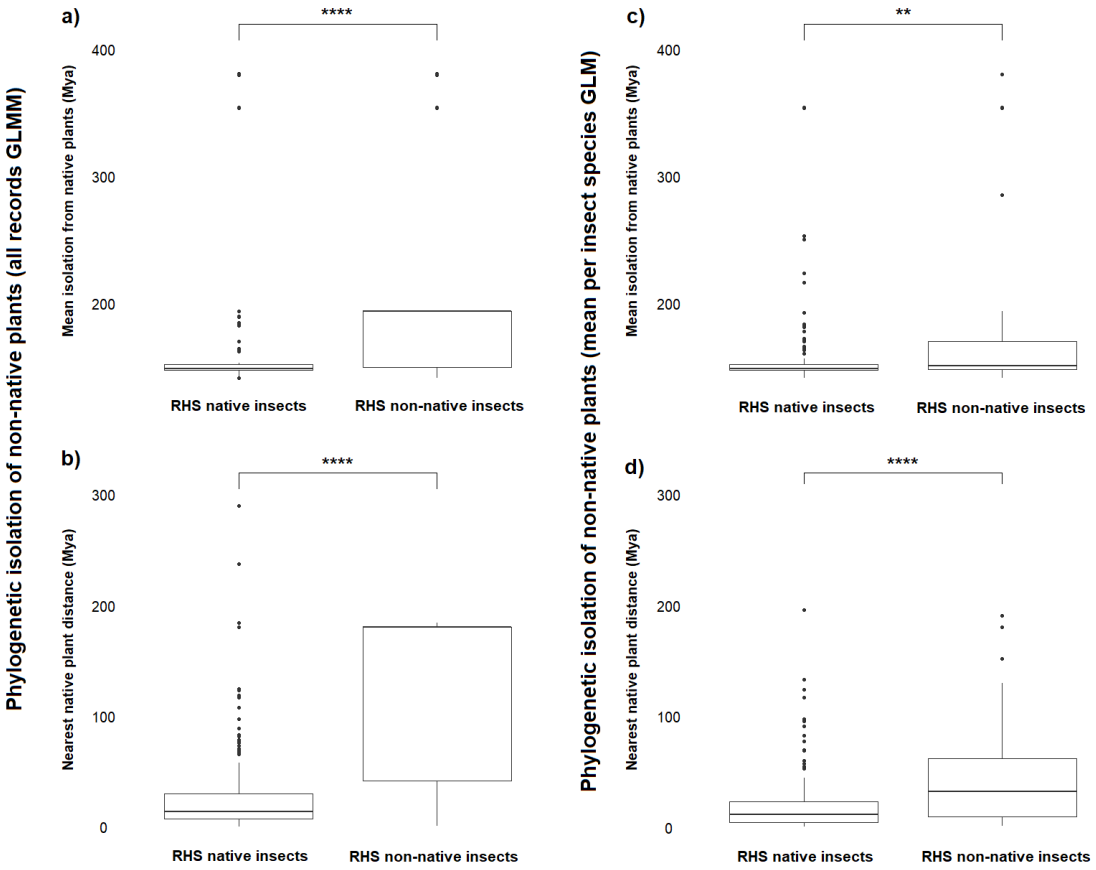

Figure 4.4: Associations of insect species with non-native host plants of varying phylogenetic isolation. RHS insects were sampled in novel garden ecosystems. GLMMs (panels a + b) analysed the phylogenetic isolation of all non-native host plants for a subset of insect genera that interacted with non-native plants 10 or more times, following standard practice for GLMM random effect sample sizes (Bolker *et al.* 2009). GLMs (panels c + d) analysed the mean phylogenetic isolation of the non-native host plants associated with each insect species. Boxplots represent median, interquartile range, and 1.5x the interquartile range. Points represent outlier records in a) and b). Points represent outlier insect species in c) and d). Significance of Tukey post-hoc contrasts NS = non-significant, ** = $p < 0.01$, **** <1e-04. Marginal pseudo R^2 represents the proportion of variance uniquely explained by insect native status in a GLMM model (panels a + b). Conditional pseudo R^2 represents the proportion of variance explained by both insect native status and insect genus (random effect) in a GLMM model (panels a + b). D^2 represents the proportion of deviance explained by insect status in a GLM model (panels c + d). d' = insect specialism. See Methods for details of the calculation of phylogenetic isolation, and the calculation of d'.

a) Gamma GLMM model (Non-Native Plant Mean Phylogenetic Isolation from Natives ~ Insect Native Status | Insect Genus) marginal pseudo R^2 = 0.055, conditional = 0.684. Number of RHS native insect records = 5563, RHS non-natives = 2073, number of insect genera = 78.

b) Gamma GLMM model (Non-Native Plant Nearest Phylogenetic Native Neighbour Distance ~ Insect Native Status | Insect Genus) marginal pseudo R^2 = 0.028, conditional = 0.448. Number of RHS native insect records = 5563, RHS non-natives = 2073, number of insect genera = 78.

c) Gamma GLM model (Non-Native Plant Mean Phylogenetic Isolation from Natives ~ Insect Native Status + d') D^2 = 0.091. Number of RHS native insect species = 314, RHS non-natives = 49.

d) Gamma GLM model (Non-Native Plant Nearest Phylogenetic Native Neighbour Distance ~ Insect Native Status + d'). D^2 = 0.095. Number of RHS native insect species = 314, RHS non-natives = 49.

4.4.3 Unique native insect communities on non-native plants

56% of native insect species in novel garden ecosystems (RHS), and 7% in the wider countryside (DBIF), were uniquely found on non-native plants (**Fig. 4.5a & 4.5c**), within these databases. The presence of unique native insect species on non-native plants in both ecosystem types was confirmed via sample based rarefaction. In the wider countryside a modelled mixed community of 1/3 natives, 1/3 archaeophytes, and 1/3 neophytes hosted a similar number of species at the reference sample size (1,812) than a community composed of only native plants (**Fig. 4.5b**). In gardens, a modelled mixed community was expected to host approximately 69 (41%) more native insect species than a native only community (at the native plant reference sample size – 1,152), despite non-native plants accumulating native insect species at a slower rate than natives (**Fig. 4.5d**).

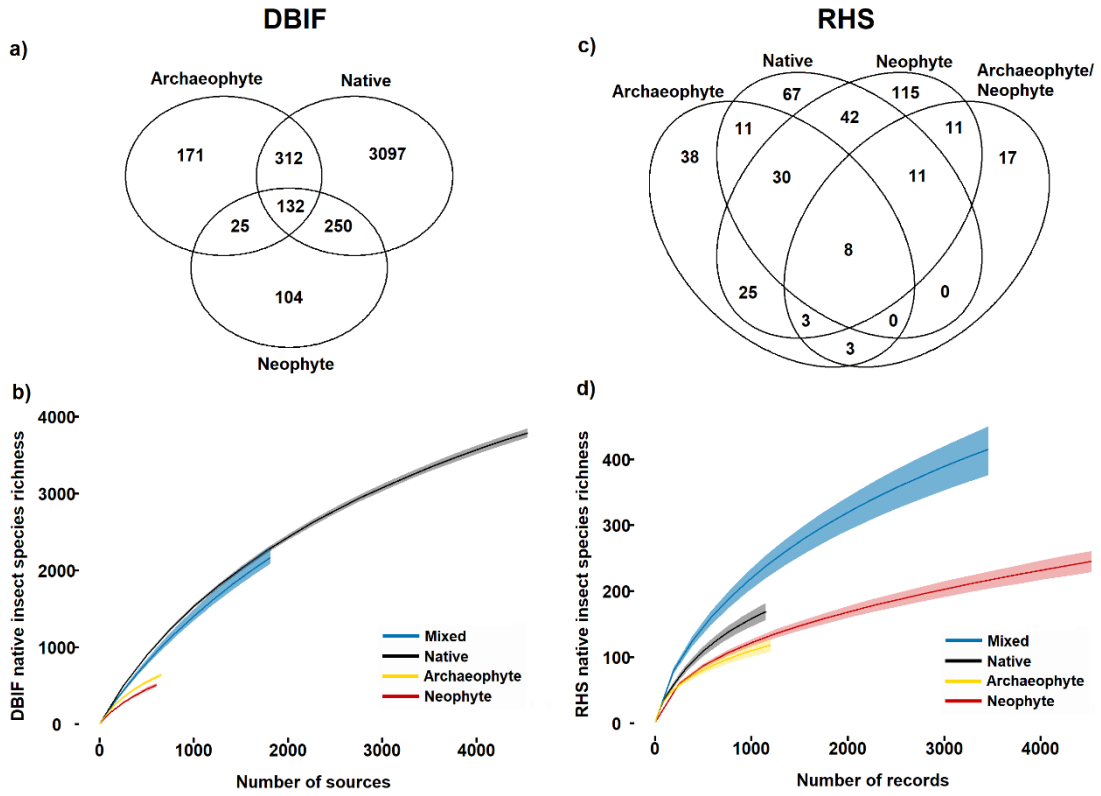

Figure 4.5: The number of native insect species unique to each plant native status in, and sample based rarefaction of the DBIF (a,b) and RHS (c,d) datasets. RHS insects were sampled in novel garden ecosystems, and DBIF insects were sampled in the wider landscape. Archaeopyte/Neophyte represents non-native plants with uncertain dates of introduction. These were excluded from the RHS rarefaction, and not present in the DBIF dataset. Rarefaction shaded areas represent 95% confidence intervals, bootstrapped 10,000 times for each plant status. Rarefaction mixed lines represents the summary of the rarefaction of 200 random samples composed of 1/3 natives, 1/3 archaeophytes, and 1/3 neophytes; the RHS upper bound is the maximum of the 200 upper 95% confidence intervals, and the lower bound is the minimum of the 200 lower 95% confidence intervals. The DBIF upper bound is the minimum of the 200 upper 95% confidence intervals, and the lower bound is the maximum of the 200 lower 95% confidence intervals. An RHS sample was defined as a unique record number and plant species combination, and a DBIF sampled was defined as a unique source and plant species combination. See Methods for details of host plant native status categories.

b) DBIF sample size of native = 4546 samples (source*plant), archaeophyte = 652, neophyte = 604, mixed = 1812.

d) RHS sample size of native = 1152 samples (record number*plant), archaeophyte = 1201, neophyte = 4531, mixed = 3456.

4.5 Discussion

Within novel garden ecosystems (RHS) there were only 29 records (<1%) of non-native insects on native plants across more than 100 years of data. Overall, non-native insects interacted with native plants far less frequently than native insects, and displayed a narrower range of native plant use. Thus, non-native insects in novel garden ecosystems are typically associating with the novel (non-native) plant habitats present there, and which they may have been introduced on (Kenis et al. 2007; Smith et al. 2007). This reinforces the wider recognition that novel anthropogenic habitats play important roles in the colonisation of new areas by non-native fauna (e.g. *Mytilopsis* mussels in marinas (Bax et al. 2001), vector mosquitoes in car tyres (Eritja et al. 2005), and *Psittacula krameri* parakeets in urban areas across Europe (Strubbe & Matthysen 2009)). Whilst the DBIF data did not permit statistical analysis involving non-native insects in the wider countryside, 78% (134/171) of non-native insect records in the DBIF occurred on non-native plants, consistent with this conclusion. However, the picture is mixed. Some non-native insects associate almost exclusively with non-native plants in 'wild' settings (Rodríguez et al. 2019), and non-native plant area is a strong predictor of spatial patterns of non-native insect establishment (Edney-Brown et al. 2018), but there is evidence that non-native insects may also associate with native plants outside of gardens (Liebhold et al. 2018). Further work is needed to clarify the interactions between non-native insects and their food plants in the wild, as the current focus is primarily on particular species of ecological and economic concern (e.g. Gilbert et al. 2004; Roy & Wajnberg 2008; Salisbury 2008).

Native insects were significantly more reliant on native plant habitats in the wider countryside (DBIF) than in gardens (RHS), a conclusion that holds when comparing across species (garden versus wider-countryside insect species) and within species (the associations of given insect species inside and outside gardens). This indicates that the native fauna may more readily associate with novel plant habitats when these novel elements occur within novel ecosystems. Native insects in the wider countryside were significantly more associated with non-native archaeophyte plants (arrival before 1500) vs. neophytes (arrival since 1500), whereas native insects in novel garden ecosystems were predominantly found on neophytes. This partly reflects the neophyte rich floral

composition of most gardens (Smith et al. 2006), but also suggests that more recently established novel plant habitats may accumulate native insect diversity more readily in disturbed (garden) than in more 'natural' ecosystems.

In gardens native insects were predominantly recorded on established non-native neophytes (present in the wild), whereas non-native insects often associated with neophytes that are exclusive to gardens (although the difference was marginal, $p < 0.01$). Many non-native insects are exclusive to horticultural settings (Kenis 2007; Smith *et. al* 2018), and so might be expected to associate with the garden neophyte ornamental plants that they are often introduced on, whereas native insects may well associate with the same non-native plant species both inside and outside gardens (253 out of 381 RHS native insects were also recorded in the DBIF). This is consistent with a pattern of many non-native insects initially establishing in gardens, and then expanding out into the countryside, and native insects colonising non-native plants where they have become established (perhaps in the countryside) and then spreading into garden environments, gradually merging the biotas.

Within novel garden ecosystems (RHS) non-native insects were found on more phylogenetically isolated novel plant habitats than native insects. If native and non-native insects are often associating with different subsets of plants this might reduce competition within gardens, thus minimising a potential negative impact of non-native insects on native insects. There was some indication that native insects in the wider landscape (DBIF) were associated with more phylogenetically isolated non-native plants than native insects in novel garden ecosystems (RHS), although the model fit poorly, and the D^2 attributed to insect native status was extremely small (0.005), making further interpretation difficult.

I found no evidence for an association of non-native insect geographical origin with novel plant habitat phylogenetic isolation. It is surprising that insects from biogeographically distant locations (in relation to Great Britain, e.g. Australasia) were not associated with more isolated non-native plants than those from closer locals (e.g. Europe/North Africa), however it may be that the number of non-native insect species from each geographical origin within the RHS dataset was too small to reveal an effect.

Comparison of insect specialism in novel garden ecosystems (RHS) and the wider landscape (DBIF) revealed opposing trends, although overall effect sizes were rather small (DBIF pseudo R^2 = 0.015, RHS = 0.067). Whilst both native and non-native insects were less specialised on novel plant habitats within novel garden ecosystems (with no interaction between insect native status and specialism), native insects were more specialised on novel plant habitats in the wider countryside. The RHS data supports previous findings that novel plant habitats accumulate a more generalist insect fauna than pre-existing native plant habitats (Brändle et al. 2008; Spafford et al. 2013; Rodríguez et al. 2019), although the DBIF results suggest that the above may not apply to insects in all ecosystem types.

Both native and non-native insects in novel garden ecosystems (RHS), and native insects in the wider landscape (DBIF), were more specialised on neophyte plants than archaeophytes, and within gardens were more specialised on garden neophytes than established neophytes. It is difficult to interpret the DBIF results, but it is possible that the effects within gardens were partially driven by the close association of some non-native insect species with the ornamental garden plants that they were introduced on (Kenis et al. 2007; Smith et al. 2007).

Insect specialists were more associated with phylogenetically isolated non-native plants in gardens (RHS) than insect generalists (in concurrence with previous findings - Grandez-Rios et al. 2015). The insects associated with phylogenetically isolated plants are often evolutionarily/ecologically distinct (Gossner et al. 2009; Padovani et al. 2020), and so may be limited in their ability to incorporate other plants into their diets. Interestingly, non-native insect specialists were more strongly associated with phylogenetically isolated non-native plants than native insect specialists. This may result from the close association of most non-native insects with non-native plants.

The presence of native insect species uniquely found on non-native plants (7% DBIF, 56% RHS) led to rarefied mixed plant communities accumulating native insect richness at a similar (DBIF) or significantly faster (RHS) rate than native-only communities, with RHS mixed plant communities hosting approximately 69 more native insect species (41% more) than native plants at the native plant reference sample size. This implies that, in addition

to accumulating non-native species (Sax & Gaines 2003; Thomas 2013a,b; Vellend et al. 2017) novel plant habitats may facilitate the re-distribution of rare native species, thus contributing to and potentially increasing native regional diversity (Padovani et al. 2020). It is important to note that a substantial proportion of native insect species unique to non-native plants within the RHS (45% of species) and DBIF (54%) datasets were only recorded once, and so it is likely that with additional sampling some of these insects would also be associated with native plants. However, consideration of the two datasets together highlights many relatively well sampled native insects unique to non-native plants (46 species [13%] with ≥ 5 records, 24 species [7%] with ≥ 10 records; see **Table A3.9** for a breakdown of insect-plant interaction frequencies). It is important to note that this effect appears to be more pronounced in native insects in novel garden ecosystems, as most records of well sampled native insects uniquely associated with non-native plants came from the RHS data (**Fig. A3.5**).

Further investigation reveals that many of the interactions in our data are well documented in Great Britain (e.g. *Kakothrips pisivorus* thrips on garden peas [*Pisum sativum*] – Gratwick 1992; *Dasineura tetensi* midges on blackcurrants [*Ribes nigrum*] – Mitchell et al. 2011; *Aceria pseudoplatani* gall mites on sycamores [*Acer pseudoplatanus*] – Chinery 2011), and demonstrates that certain native insects can be closely associated with non-native plants (Shapiro 2002; Tallamy & Shropshire 2009; Jones & Leather 2012; Ramírez-Restrepo et al 2017; Koyama et al. 2018). Interestingly, each of the above example insects shares a name, either colloquially or in Latin, with their non-native host plants. This is also true for other insects in **Table A3.9** (e.g. *Smynthurodes betae* [bean root aphid] on *Phaseolus coccineus* [runner bean], *Delia antiqua* [onion fly] on *Allium cepa* [onion], and *Unaspis euonymi* [Euonymus scale] on *Euonymus japonicus* [Japanese spindle]), although there are also many examples where this is not the case (e.g. *Phytonemus pallidus* [cyclamen mite] on *Aster amellus* [Italian aster], *Bryobia praetiosa* [clover mite] on *Ribes uva-crispa* [gooseberry], and Saissetia coffeae [hemispherical scale] on Nerium oleander [oleander]). Given that some insect histories are not particularly well studied, there is a possibility that some of the 'native' insects in our datasets (that share names with their non-native hosts) are actually non-native insects introduced with non-

native plants. However, the Great Britain Non-Native Species Information Portal (NNSS 2019) is the most comprehensive guide to non-native species in Britain, and its accuracy can be confirmed through the National Biodiversity Network Atlas (NBN Atlas 2020), which lists every insect species included in **Table A3.9** as native in Britain. Thus, it is highly unlikely that a significant number of non-native insects have been erroneously labelled as native in our data. Instead, these insects have been named after their predominant associations with non-native plants.

To conclude, both native and non-native insects associate with novel plant habitats in novel garden ecosystems (RHS), although non-native insects are particularly reliant upon them. In the wider countryside (DBIF) native insects associate with more native plant habitats compared with their conspecifics in novel garden ecosystems. Insect specialism and novel plant habitat distinctiveness can both modulate the accumulation of native and non-native insects, and I find no evidence for an influence of non-native insect origin on novel plant habitat associations. 48% of all interactions across both datasets were novel (involving either non-native plants or insects), and of those novel interactions 78% consisted of native insects on non-native plants. This highlights the ecological significance of novel interactions, and the potential value of novel plant habitats to support native biodiversity in a rapidly changing Anthropocene world. Of course, not all non-native plants are beneficial (from various human perspectives), and so it is vital that we consider any potential negative impacts when determining the conservation value of a novel plant habitat.

In summary:

i) Novel plant habitats (non-native plants) have a large influence on the accumulation of non-native insect diversity in new regions, with non-native herbivorous insect species in novel garden ecosystems almost exclusively associated with novel plant habitats.

ii) Non-native insect species associate with more phylogenetically distinctive novel plant habitats than native species.

iii) Novel plant habitats may be colonised by more specialist (DBIF) or more generalist (RHS) insect species, depending on the ecosystem type (wider countryside vs. novel garden ecosystems).

iv) Specialist insects in novel garden ecosystems associate with more phylogenetically isolated non-native plants (RHS), although this effect is not apparent in the wider landscape (DBIF).

v) Native insect biodiversity is strongly influenced by the presence of novel plant habitats, especially within highly modified garden ecosystems. Novel plant habitats may facilitate the re-distribution of native insect species that are otherwise rare on native plants, thus contributing to, and potentially increasing native regional diversity.

4.6 Acknowledgements

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Chapter 5 General Discussion

A natural calcareous grassland habitat

A novel Anthropocene brownfield habitat

5.1 Summary of thesis findings

In this thesis I have presented the accumulation of insects on non-native plants as a novel, readily available, highly replicated, and ecologically important model system that can better our understanding of the accumulation of diversity in anthropogenic novel habitats. I have demonstrated that non-native plants generally host depauperate insect communities, although these reductions in α-diversity are significantly influenced by non-native plant phylogenetic isolation, range size, and time since arrival in Great Britain. Non-native plants are strongly associated with non-native insects, and so may facilitate their spread (potentially leading to negative economic and ecological consequences if the insects are invasive). However, there is considerable evidence that non-native plants can support native insect biodiversity, particularly in novel garden ecosystems. Taking an Anthropocene perspective, my research suggests that novel habitats are likely to have an important role in the conservation of native species, although various factors (such as the distinctiveness of novel habitats from pre-existing habitats) will influence their capacity to accumulate species. Overall, non-native plants and novel habitats may provide an array of ecosystem services, although caution is required regarding potential ecosystem disservices.

Below I present a brief summary of **Chapters 2**, **3**, and **4**, from the perspective of insect-plant ecology. **Sections 5.2.1-5.2.3** discuss the wider implications of my results, and consider the balance of positive and negative impacts of non-native plants on insect biodiversity. In **section 5.2.4** I consider the relevance of my research with respect to the accumulation of biodiversity in anthropogenic novel habitats. Finally, in **section 5.3** I review potential avenues for future research, and in **section 5.4** I provide my final conclusions.

In **Chapter 2** (*Documenting a century of British invertebrates on plants: The RHS and the DBIF*) I outlined the extensive work that I carried out to develop the geographic-scale Database of Insects and their Food Plants (DBIF), and the Royal Horticultural Society Entomology Advisory Database (RHS). In addition to substantially cleaning both datasets and standardising to current nomenclature, I associated British native statuses with all

invertebrate and plant species. Together the RHS and the DBIF report 138,648 interactions between primarily phytophagous insects and plants recorded mostly in Great Britain over the past century, both in gardens (RHS) and the wider landscape (DBIF). Taxonomic coverage within both datasets is relatively broad, although there is a large emphasis on insects over other invertebrates, and most of the records detail herbivorous interactions, with little representation of other trophic groups. Collectively the RHS and the DBIF represent one of the largest sources of British invertebrate-plant interactions that is currently available, and can make an important contribution to a wide array of research in diverse fields, such as global change biology, conservation biology, and a range of ecological topics (e.g. population, community, network, macro and evolutionary ecology). Both datasets will be made freely available for download and re-use when **Chapter 2** is published in a peer reviewed journal, whereas currently there are certain restrictions upon their usage.

In **Chapter 3** (*Introduced plants as novel Anthropocene habitats for insects*) I analysed a species level subset of the DBIF (excluding all records resolved to the genus level or above). Additionally, I incorporated data from local-scale sampling of pollinators and other plant-associated insects on experimental plots at the Royal Horticultural Society's Wisley Garden. The following results are particularly relevant for native insect communities, as the vast majority of insects in both datasets were native (98% in the DBIF, 97% in the Wisley pollinator samples, and 99% in the Wisley Vortis samples; percentages based on the taxa identified to species level and of known native status). Overall, non-native plants hosted less rich and abundant insect communities, especially if they were phylogenetically isolated from native plants. However, there were many insect species that were uniquely associated with non-native plants. Furthermore, sampled based rarefaction revealed that mixed plant communities (1/3 natives, 1/3 non-native archaeophytes/congeners, and 1/3 non-native neophytes/exotics) accumulated insect species at a similar rate than native-only communities. Interestingly, there was no difference in how various trophic levels responded to host plant native status and phylogenetic isolation, with further work required to determine whether this applies more broadly in other systems. The effect of host plant phylogenetic isolation depended on insect specialism, as relatively generalist

pollinators were more influenced by the mean isolation of a plant from all other plants within the community, whereas more specialised plant-associated insects responded to the phylogenetic distance between a plant and its closest phylogenetic neighbour. Finally, insect α-diversity was positively affected by non-native plant range size, and by the time since a non-native plant's introduction (archaeophytes arriving before 1500 versus neophytes arriving after 1500), although the size of both effects was small in comparison with the effect of sampling effort.

Chapter 4 (*The development of Anthropocene biotas: colonisation of novel plant habitats by native and non-native insects*) made use of species level subsets of the phytophagous insects in the RHS and the DBIF, and revealed that non-native plants (particularly those that were phylogenetically isolated) were strongly associated with non-native insects. Insect specialists in novel garden ecosystems (RHS) were more associated with native plants, whilst specialists in the wider landscape (i.e. more 'natural ecosystems – DBIF) were more associated with non-native plants. Insect specialists tended to visit more phylogenetically isolated non-native plants in gardens, although effect sizes were small, and no effect was detected in the wider landscape. Importantly, there were many native insects that were uniquely associated with native plants, particularly in novel garden ecosystems versus the wider landscape. Furthermore, mixed garden plant communities (1/3 natives, 1/3 non-native neophytes, and 1/3 non-native archaeophytes) accumulated native insect species at a higher rate than native-only communities.

5.2 Non-native plants and novel anthropogenic habitats

5.2.1 Negative impacts of non-native plants

In **Chapter 3** I demonstrated that non-native plants generally host less rich and less abundant insect communities, although this is dependent on their phylogenetic distance from native plants. Insect α-diversity was lower on phylogenetically isolated non-native plants, and this effect was detected when phylogenetic isolation was represented both categorically (i.e. exotic non-native plants distantly related to natives versus congeneric

non-natives) and continuously (i.e. phylogenetic divergence time in millions of years). Native phytophagous insects were particularly unlikely to use phylogenetically isolated non-native plants (compared with non-native phytophages – **Chapter 4**), and disproportionately colonised non-native plants that were more closely related to native plant species (in gardens – RHS). Overall, these results indicate that phylogenetically distinct non-native plants may have a negative impact on local-scale native insect biodiversity in the areas to which they are introduced, as native insects may struggle to colonise, and will establish less rich and less abundant communities when they do colonise. Such reductions in insect diversity may then impact other animal groups that feed on insects, for example, insectivorous bird abundance may be decreased on non-native plants due to a lower biomass of prey caterpillars (Narango et al. 2017).

Many authors have revealed reduced numbers of insects on non-native plants, for example showing decreased insect richness and abundance on non-native plants compared with native plants (Bezemer et al. 2014; Meijer et al. 2016) and in habitats dominated by non-native plants versus natural habitats (Buchholz et al. 2015; Ramula & Sorvari 2017). In contrast, very few consider the influence of host plant phylogenetic isolation. It is essential to include host plant phylogenetic isolation in any analyses that quantify insect biodiversity on non-native plants, as my results and the literature (Spafford et al. 2013; Grandez-Rios et al. 2015) suggest that isolated non-native plants may struggle to support native insects. It is also important to consider multiple measures of phylogenetic isolation. In **Chapter 3** I revealed that insect generalists and specialists responded differently to mean host plant phylogenetic isolation and nearest phylogenetic neighbour distance. This indicates that, depending on the insect species/groups that are in question, significant effects may be missed by only employing a single measure.

In **Chapter 4** I clearly demonstrated a high degree of association between non-native phytophagous insects and non-native garden plants, with only 29 out of 2,071 (<1%) non-native insect individuals occurring on native garden plants. It was not possible to formally analyse the host plant associations of non-native insects in the wider landscape as non-native insects were poorly represented in the DBIF. However, 78% (134/171) of non-native insects in the DBIF occurred on non-native plants, suggesting that there is also a strong

association between non-native insects and non-native plants in the wider countryside (albeit not as strong as in gardens). This is consistent with other evidence: some non-native insects also typically associate with non-native plants outside of gardens (Sugiura et al. 2007; Rodríguez et al. 2019), and spatial patterns of recently established insect species are explained by non-native vegetation cover (Edney-Browne et al. 2018). Overall, my research confirms the importance of non-native plants for the establishment of insects in new regions, as horticultural trade (particularly trade in ornamental plants) is responsible for the majority of insect introductions globally (Kenis et al. 2007; Smith et al. 2007; Liebhold et al. 2012). This means that non-native plants that are well-suited to accumulate native biodiversity (due to having low phylogenetic isolation from native plants, large ranges, and increased time since introduction) might still have negative impacts as they can enable the establishment of invasive insects. Invasive insects have a range of negative economic and ecological impacts, such as the destruction of ornamental, agricultural, and wild plants through unchecked herbivory (Dodds & Orwig 2011; Bradshaw et al. 2016; Lovett et al. 2016), or severe competition with, and predation of, native insect species (Roy et al. 2016; Potts et al. 2016). Invasive insects may also have adverse consequences for human and animal health (Roques et al. 2009). However, the vast majority of introduced insects are not invasive, and have few economic or ecological impacts (Roy et al. 2012; Smith et al. 2018). This distinction underlies the importance of extensive sampling of the insect communities associated with non-native plants when determining whether they pose a risk.

5.2.2 Positive impacts of non-native plants

In **Chapter 3** I established that phylogenetically distinct non-native plants hosted unique insect communities, and that non-native plants were often associated with insect species that were not found on native plants within the DBIF or on the Wisley experimental plots. In **Chapter 4** I focused specifically on native insects, and confirmed that a large number of phytophagous native insects in the wider landscape (DBIF), and especially in gardens (RHS), were uniquely associated with non-native plants. It is highly likely that these native insects occur on native plants somewhere in Great Britain, although the absence of such interactions in the RHS and the DBIF suggests that non-native plants are supporting native

insects that are rarely found on native plants at a regional scale. This may explain why a modelled mixed community of native and non-native plants supported increased native insect richness compared with a native-only community in gardens (RHS), and similar native insect richness in the wider landscape (DBIF).

In addition to uniquely hosting certain native insects, some non-native plants hosted high insect richness and abundance (**Chapter 3**). Non-native plants that were closely related to the native flora supported similar levels of insect α-diversity to native plants, or even, on occasion, hosted more rich and abundant insect communities. For example, the abundance of plant-associated insects on the Wisley experimental plots was approximately 75% higher on the non-native plant *Lythrum virgatum* (which was closely related to the native flora) when compared with the next most abundant insect community found on the native plant *Molinia caerulea*. Overall, these results re-affirm that phylogenetic isolation may significantly influence the capacity for a non-native plant to support native insect biodiversity (see **section 5.2.1**).

Despite some uncertainty about overall global trends of insect abundance, biomass, and species richness (Simmons et al. 2019; Thomas et al. 2019), there is no question that some insect populations are in decline (Hallmann et al. 2017; Lister et al. 2018; Seibold et al. 2019). Therefore, it is essential that conservation practitioners consider the potential for non-native plants to support native insect diversity. There are multiple examples of native insects relying on non-native plants in the absence of their original native hosts or food plants, such as butterflies in urban gardens (Shapiro 2002; Jones & Leather 2012; Ramírez-Restrepo et al. 2017) and honeybees in suburban ecosystems (Koyama et al. 2018). Furthermore, some authors have also found similar or increased native insect richness and abundance on some non-native plants compared with native plants (Novotny et al. 2003; Sugiura et al. 2007; Harvey et al. 2013; Salisbury et al. 2017). In **Chapter 4** I demonstrated that many phytophagous native insect species shift from exclusive associations with native plants in the wider landscape (where native plants are typically in the majority – Thomas & Palmer 2015) to non-native plants in gardens (where non-native plants are often in the majority – Loram et al. 2008). This confirms that native insects may rely on non-native plants in habitats where their native plant hosts are no longer present or are greatly

reduced. It also indicates that British domestic gardens (and the non-native plants within them) can provide sufficient resources to support native insect species from the wider landscape (Smith et al. 2006).

In addition to potentially supporting native insects in specific locales/regions, non-native plants can provide an array of other ecosystem services. For example, certain non-native plants facilitate the restoration of native tree species and subsequent forest regeneration (Lugo 1997), they may remediate environmental contaminants (Rai & Kim 2020), they can serve as biological corridors enabling invertebrates to move between isolated hosts (Van der Colff et al. 2015), and may rapidly produce biomass for use in biofuels (Yadav et al. 2013). Furthermore, some non-native insects (which are often introduced with non-native plants – as discussed in the previous section) may also provide a variety of ecosystem services (Schlaepfer et al. 2011). For instance, certain introduced insects pollinate native plants in the absence of native pollinators (Dick 2001; Gross 2001), they may consume urban food waste (Youngsteadt et al. 2015), and can control invasive non-native plant species (Morrison et al. 1998). It is vital that we recognise the role that non-native plants and insects play in ecosystem services such as these, as non-native species are predicted to be increasingly important for the provision of ecosystem services in future (Williams 1997; Ewel & Putz 2004; Tassin & Kull 2015).

5.2.3 Time since introduction and range size

In **Chapter 3** I determined that non-native plants with a small geographic range may support relatively few phytophagous insect species compared with plants with larger ranges. I also revealed that non-native plant range size and phylogenetic isolation operate in tandem, and with a similar strength, to influence insect richness on non-native plants. The effect of range size on the herbivore richness associated with native and non-native plants is well-established (Kenendy & Southwood 1984; Lawton et al. 1993; Andow & Imura 1994; Brändle & Brandl 2001; Brändle et al. 2008), although very few authors have considered range size alongside phylogenetic isolation (Branco et al. 2015). It is important to note that whilst non-native plants with a larger range may generally host more insect species, non-native plants may negatively impact native plant biomass, reproduction, and survival through resource competition (Jauni & Ramula 2015), and through competition

for pollinators (Dietzsch et al. 2011). This means that an increase in their range might be to the overall detriment of native insect biodiversity (as native plants generally support more rich and abundant insect communities – as discussed above).

There is considerable evidence that herbivore richness increases with time since non-native plant introduction (Kennedy & Southwood 1984; Brändle et al. 2008; Kirichenko & Kenis 2016), although an effect is not always detected (Andow & Imura 1994). Furthermore, some have concluded that the effect of time asymptotes within the first few centuries post establishment, after which further increases in species richness are better predicted by range size (Strong 1974; Strong et al. 1977). I failed to detect an effect of time within a few centuries (by testing the year of non-native neophyte introduction since 1500), and instead observed accumulation over longer time-scales (Brändle et al. 2008), with higher richness on non-native archaeophytes (introduced before 1500) versus non-native neophytes (**Chapter 3**). Non-native plant range size continued to have a significant effect when included in the same model as non-native neophyte/archaeophyte status, suggesting that time and range size operate in tandem. It is important to consider that the absence of accumulation in shorter-time scales may be due to the fact that the DBIF data is a collation of the entomological literature, and the activity of entomological/biological recorders has generally increased over time. Furthermore, a small effect of neophyte introduction date may have been overshadowed by the very large effect of sampling effort, as sampling effort dominated all models of DBIF insect richness.

The positive influences of non-native plant range size and time since introduction on insect richness are evident when examining the ten non-native plants that hosted the highest insect richness within the DBIF. These are: *Salix alba* – white willow (89 associated species), *Pyrus communis* – European pear (70), *Acer pseudoplatanus* – sycamore (67), *Prunus domestica* – European plum (67), *Picea abies* – Norway spruce (52), *Salix viminalis* – basket willow (45), *Triticum aestivum* – bread wheat (45), *Salix fragilis* – crack willow (44), *Artemisia vulgaris* – mugwort (41), and *Larix decidua* – European larch (36). These plants hosted a mean of 55.6 insect species, which is far above the mean number of species hosted by all non-native plants (8.3) and by native plants (10.1). The mean number of hectads occupied in Great Britain by these non-native plants was 1529.8, which is

considerably higher than the mean for all non-native plants of 951.0, highlighting the importance of range size. Seven of the ten plants are archaeophytes, although only one third of the plants within the DBIF are archaeophytes (120 archaeophytes, 234 neophytes), emphasising the importance of time since introduction. Interestingly, seven of the ten plants are trees. It may be that non-native trees support increased insect richness compared with smaller non-native species (such as shrubs or herbaceous perennials), due to the positive correlation between plant size and herbivore richness (Kennedy & Southwood 1984; Brändle & Brandl 2001). Importantly, the mean number of sources reporting on these plants (29.0) was much higher than for most non-native plants (5.6). This emphasises the need to control for sampling effort within multivariate models.

5.2.4 Biodiversity in anthropogenic novel habitats

Taking a wider Anthropocene perspective, my results suggest that novel habitat age (represented by time since non-native plant introduction) and habitat area (non-native plant range size) have a positive influence on associated α-diversity. Whilst novel habitats may host decreased α-diversity compared with pre-existing habitats, this difference is modulated by novel habitat distinctiveness (non-native plant phylogenetic isolation). This suggests that novel habitats that present similar attributes to pre-existing habitats (such as physical structure, microclimate, and biochemical composition) may potentially support a similar number of individuals and species, whilst those that are particularly divergent may host depauparate communities. A number of authors have confirmed the positive effect of novel habitat age on associated diversity (Nichols & Nichols 2003; Cramer et al. 2008; Li et al. 2014), although none have, to my knowledge, attempted to quantify the distinctiveness of a novel habitat from pre-existing habitats. This is likely due to the unique and complex nature of each novel habitat type (such as mine tailings, old fields, and green rooves) and how they differ from pre-existing habitat types. Researchers should take a multivariate approach to quantify novel habitat distinctiveness, as it is unlikely that a single continuous measure (equivalent to the phylogenetic isolation of non-native plants) can function as a proxy for distinctiveness in most novel habitat types. Relevant variables include: i) physical structure, for example, differences in verticality, the size, shape, and complexity of physical niches provided by both the abiotic and biotic environment, and the influence

that structure has on the movement of species into and across a habitat; ii) overall climate and the microclimates associated with each niche within a habitat; iii) the chemical composition of the soil, water, atmosphere, and the biosphere; iv) the likelihood, frequency, and rate of change i.e. disturbance of all of the above. Whilst quantifying the above attributes is not a simple task, I would argue that it is necessary in order to definitively compare a novel habitat with a pre-existing one, and should improve the quality of any comparative analyses.

The extreme prevalence of non-native insects on non-native garden plants confirms the association of non-native species with novel habitats (McKinney 2002; Lugo & Helmer 2003; Bonter et al. 2010), and the potential for novel habitats to facilitate the colonisation of new areas by non-native species (Bax et al. 2001; Eritja et al. 2005; Strubbe & Matthysen 2009). This might be particularly true for novel habitats that are distinctive compared with pre-existing habitats, as non-native phytophagous insects were associated with more phylogenetically isolated non-native plants than native insects. It is important to consider that the potential to facilitate colonisations is only an issue if the non-native colonists in question are harmful (and in most cases they are not, for example in Great Britain only 8% of non-native species are considered to have a negative ecological impact - Roy et al. 2012). Nonetheless, novel habitat creation is dependent upon the destruction of existing habitats, leading to an array of ecosystem disservices such as the loss of endemic species (World Resources Institute 2005), and limitations to the dispersal of others through the loss of suitable habitat corridors (Fletcher et al. 2018).

Some non-native plants were associated with a high diversity of native insect species, and with native insects that were not found on native plants (within our datasets). This suggests that novel habitats may provide a significant ecosystem service by supporting native species in the absence of suitable pre-existing habitats. There are multiple examples of novel habitats supporting native biodiversity, e.g. urban street trees facilitate range expansion of Grey-headed Flying fox *Pteropus poliocephalus* (Williams et al. 2006), urban gardens support bird diversity (Davies et al. 2009), brownfield sites provide habitats for range expanding *Thymelicus sylvestris* butterflies (Gilchrist et al. 2016) and rare beetles (Eyre et al. 2003), golf courses help preserve a variety of fauna of conservation concern

(Colding & Folke 2009), and the species richness of bees and butterflies is higher in railway embankments than in typical semi-natural grassland habitats (Moroń et al. 2014). In addition to supporting native species, anthropogenic novel habitats may also provide an array of other ecosystem services, such as climate regulation, nutrient cycling, and the provisioning of biochemical resources, and the overall quality of these services is often increased compared with pre-existing habitat baselines (Evers et al. 2018).

To conclude, it is generally preferable to avoid the destruction of natural habitats, and the consequent creation of novel habitats. However, this is becoming more difficult as the Anthropocene progresses, and many ecosystems become increasingly novel compared with historical baselines (Radeloff 2015). Novel habitats are here to stay, and so understanding more about the ecosystem services and ecological communities associated with them is vital as we 'adapt' to a changing world. In addition to looking at novel habitat age and area as key determinants of associated diversity, I recommend that researchers attempt to quantify the distinctiveness of a novel habitat by measuring key indicators that determine its physical structure, climate, and chemical composition. This might help practitioners to combat potential disservices (including the introduction of invasive species), and to enhance the quality of novel habitats as resources for native biodiversity. Certain novel habitats may have a high potential to support native biodiversity, both currently and in future. For example, many of today's priority habitats for conservation in the UK, such as lowland heaths and downland, were originally novel habitats.

5.3 Limitations and recommendations for future research

5.3.1 Insect specialism

In **Chapter 4** I considered the relationship of phytophagous insect specialism with host plant native status and phylogenetic isolation, with contrasting results emerging from gardens and the wider landscape. There was a weak positive relationship between host plant phylogenetic isolation and insect specialism in the RHS garden data (mirroring trends observed by Brändle & Brandl 2001; Grandez-Rios et al. 2015), whilst there were no

significant effects in the wider landscape DBIF data. Additionally, whilst generalist insects in gardens were more associated with non-native plants than specialists (concurring with Brändle et al. 2008; Spafford et al. 2013; Rodríguez et al. 2019), in the wider landscape the insects on non-native plants were more specialised. Such disparate results suggest that further research is needed to clarify the ecological mechanisms that determine the association of insect specialists with non-native plants. If non-native plants truly favour generalist insect species then their prevalence in an area may negatively impact the survival of more specialised insects.

5.3.2 Herbivore damage

I did not specifically investigate herbivore damage in my thesis, although in **Chapter 3** I considered herbivore abundance on non-native plants, and abundance and damage are often linked (von Sydow 1997; Hartley et al. 2010). There is evidence that non-native plants can suffer varying levels of herbivore damage when compared with native plants, and some authors have concluded that herbivore damage is similar on non-native plants, despite decreased herbivore abundance (Bezemer et al. 2014). This might be because herbivores have a greater per capita effect on non-native plants than on native plants. Future research might investigate this phenomenon through the design of a controlled laboratory feeding experiment investigating per capita feeding. However, in the absence of competing herbivores and higher trophic levels, such an experiment might struggle to reliably model a natural native/non-native plant-herbivore system.

5.3.3 Multitrophic invertebrate communities

In **Chapter 3** I revealed that non-native and/or phylogenetically isolated plants generally hosted fewer insect species and individuals of all feeding types (herbivore, detritivore, omnivore, and predator). There is evidence that higher trophic levels often relate to non-native plants in a similar manner to insect herbivores (Spafford et al. 2013; Salisbury 2017), and this might be expected given that the natural enemies of herbivores also rely on the chemical and visual cues associated with food plants to find their hosts or prey (Harvey 2010). However, other trophic levels do not always respond to non-native plants in the same manner as herbivores (Fortuna et al. 2013; Salisbury 2017; Clem & Held 2018).

If non-native plants are either more or less attractive to higher trophic levels this could lead to a shift in the balance of predators and parasites versus prey and hosts, resulting in either decreased (Kennedy & Southwood 1984; Lewinsohn 2005; Meijer et al. 2016) or increased (Novotny et al. 2003; Sugiura et al. 2007; Harvey et al. 2013) numbers of herbivores on non-native plants. My data from the Wisley experimental plots did not indicate any trophic level shifts, and I was not able to test for such effects within the geographic-scale RHS and DBIF databases as they were composed almost entirely of phytophagous insect-plant interactions. More resounding conclusions might be reached with multitrophic datasets of a similar temporal and spatial scale to the DBIF and the RHS, although I am not currently aware of any such resources. Additional data would also enable examination of the effects of non-native plant range size and time since introduction on insects from other trophic levels. I was unable to do so using the multitrophic Wisley experimental plot data, as introduction dates and range sizes are generally unavailable for garden plants. In **section 5.3.8** I discuss the potential for citizen science to generate new large datasets that might fill this gap.

5.3.4 Non-native plants and pollinators

In **Chapter 3** (Wisley experimental plot data) I calculated the mean specialism of the pollinator and other plant-associated (Vortis sampled – primarily herbivorous) insect communities associated with non-native plants. I revealed that the richness and abundance of pollinators and Vortis insects were differentially influenced by non-native plant phylogenetic isolation. Whilst both pollinators and Vortis insects were affected by the distance from a non-native plant to its nearest phylogenetic neighbour, only pollinators responded to the mean distance from a non-native plant to all of the other plants in the phylogeny. Future work might consider whether these differences are mirrored at the geographic-scale. I was unable to do so using the RHS or the DBIF, as both datasets include primarily phytophagous interactions.

Given the limited taxonomic resolution of some of the Wisley pollinator data (35 taxa at species level, genus = 5, family = 5, superfamily = 1, infraorder = 2, suborder = 1, order = 5) I did not consider the specialism of individual taxa. Examination of the relationship between pollinator species' specialism, plant native status and phylogenetic isolation

would make an interesting avenue for future work. My results from **Chapter 4** suggest that both plant native status and phylogenetic isolation may influence the associations of specialist herbivores with plants, and there is evidence that specialist pollinators do not typically visit non-native plants (Memmott & Waser 2002; Tepedino et al. 2008). This suggests that specialist pollinators might be disproportionately negatively affected by the spread of non-native plants to new locales/regions.

Further work might also consider the effects of time since non-native plant introduction and non-native plant range size on pollinator diversity. This was not possible using the RHS and DBIF databases (as they feature primarily phytophagous interactions). Additionally, I could not use the RHS database and the Wisley experimental plot data due to limited availability of garden plant introduction dates and range sizes. There are indications that the pollinator species richness associated with non-native plants increases with both time and range size (Pyšek et al. 2011), although very few authors consider these effects on pollinators. Contrastingly, the effects of time since non-native plant introduction and range size are relatively well-studied for insect herbivores.

5.3.5 Insect accumulation during the early years

I found no evidence that phytophagous insect richness increases with time since neophyte introduction to Great Britain, although I did find evidence for accumulation on longer time scales (non-native archaeophytes were associated with more insect species than non-native neophytes – **Chapter 3**). Whilst the absence of accumulation on shorter time scales may be genuine, it may have resulted from biases in the activity of entomological recorders, or the effect of time may have been obscured by the dominance of sampling effort as a predictor in models of DBIF insect richness. Furthermore, sample breadth was limited because it was not possible to test for the effect of time using the Wisley experimental data or the RHS database (reliable introduction dates are not available for most garden plants). Others have documented significant accumulation of insect diversity during the first centuries post establishment (e.g. Hawkes 2007; Kirichenko & Kenis 2016), although accumulation during the first decades is rarely observed. Future research might benefit from the design of a carefully controlled experiment tracking insect accumulation during the very first years following the arrival of non-native plants to a new region.

Careful design would be necessary to avoid the accidental introduction of plants to new areas, for instance by using plants that are unable to persist naturally outside of the experimental site. Inclusion of phylogenetically diverse plants in the experiment would enable testing of the influence of non-native plant phylogenetic isolation on insect accumulation, and a broad sampling strategy could track the accumulation of insects from multiple trophic levels.

5.3.6 Proximity of non-native plants to colonist pools

I did not have sufficient data to test for effects of the proximity of non-native plants to pools of potential colonists (i.e. related native plants), and investigation of this is distinctly lacking from the literature. If non-native plants are viewed as potentially colonisable habitat patches for plant-associated invertebrate populations, then metapopulation theory (Hanski 1998) would predict that the closer a non-native plant is to related native plants, the more easily it will be colonised. Of course, lots of other factors are also important, such as the composition of the matrix between native and non-native plant habitat patches. But, all things considered, it might be expected that geographic proximity to related native plants would be positively correlated with insect diversity on non-natives, and with the speed at which diversity on non-natives accumulates over time. It is also likely that the geographic proximity between non-native plants and related native plants is negatively correlated with the β-diversity (dissimilarity) of the invertebrate communities found on those plants. The relationship between the geographic proximity of native and non-native plants and various measures of diversity on non-native plants would make a very interesting avenue for future research. Difficulties in obtaining sufficient geographic coverage to make robust conclusions may be the reason for the absence of such studies in the literature, but might be overcome through the use of citizen science (see section 5.3.8).

5.3.7 Considering impacts on different scales

My thesis focused on the effects of non-native plants on insect diversity at the community level (i.e. species richness, abundance, and community composition). Whilst community level studies elucidate many of the effects of non-native plants on insect biodiversity

overall, future research might benefit by considering impacts at other scales, for instance at the larger-scale ecological network level. The presence of non-native plants can lead to significant changes to plant-pollinator network structure (Kaiser-Bunbury et al. 2011; Albrecht et al. 2014), although in other cases it may have little effect (Padrón et al. 2009; Vilà et al. 2009). Although many authors consider the effects of non-native plants on plant-pollinator networks, few examine networks that include other plant feeding insects, and insects from higher trophic levels. There is some evidence that plant invasions may influence multitrophic network interaction evenness, although other effects on network structure are highly variable (López-Núñez et al. 2017).

Non-native plants may also have impacts at the individual insect level, although consideration of smaller-scale individual effects is lacking for both pollinators and other plant-associated insects. Non-native plants may impact the survival and fitness of individual insects by influencing their behaviour, nutrition, and health, revealing more nuanced effects which are not detected at the community level (Stout & Tiedeken 2017). For instance, whilst *Rhododendron ponticum* is toxic for honeybees and some solitary bees in its introduced range the survival of native bumblebees is not affected (Tiedeken et al. 2016). This may explain why bumblebees flourish in sites invaded by *R. ponticum* (Stout et al. 2016).

5.3.8 The power of biological recording and citizen science

Citizen science has been vital to this work. Aside from the Wisley experimental plot data in **Chapter 3**, all my analyses relied on the RHS and DBIF geographic-scale databases. It is due the efforts of countless amateur and expert entomologists, horticulturalists, and citizen scientists that the RHS and the DBIF exist, and will soon be more widely available for further re-use when I publish **Chapter 2** as a data paper. Whilst local-scale experiments such as those at Wisley provide an effective means to systematically test specific ecological hypotheses, the temporal, spatial, and taxonomic scale of the data that can be collected pales in comparison with that which is available through large-scale datasets such as the RHS and the DBIF. Whilst there were obvious limitations and biases within the RHS and the DBIF, such as the lack of a multitrophic focus, they provided me with a vast well of information with which to draw some resounding conclusions. Others have also

benefited from them, as the RHS and the DBIF have contributed to a number of publications on diverse topics such as insect species' distribution and host range changes (e.g. Salisbury & Malumphy 2017; Plant et al. 2019; Tuffen et al. 2019), and the evolutionary history of phytophagous insects (and mites) and their food plants (Ward et al. 2003). Future research would certainly benefit from their continued use, whilst the creation of new large-scale datasets considering aspects that are missing from the RHS and the DBIF, such as the host plant associations of non-native insects in the wider landscape, might be facilitated by citizen science.

Citizen science is being increasingly recognised as an invaluable tool that enables research at far larger scales than would be otherwise possible (Sutherland et al. 2015; Bartomeus & Dicks 2019). Furthermore, the potential scale of research is likely to continue to increase, as a result of the substantial advances in information technology and the growth of citizen science social media platforms (e.g. the iSpot project – http://www.ispotnature.org). Given such growth, it is important that we maximise the potential of citizen science by ensuring that data are open access, and that common basic protocols ensure that data are as comparable as possible among related projects (Bartomeus & Dicks 2019). Whilst it is true that recording of certain difficult species groups will continue to rely on a small number of highly skilled volunteers (Pocock et al. 2015), many aspects of citizen science require little specialist knowledge. Thus, citizen science is an effective and accessible means to engage the public with the scientific process (Silvertown 2009). This wider engagement is vital as our planet faces ecological and environmental challenges on an unprecedented scale.

5.4 Conclusions

Widespread ecosystem alteration, and the subsequent creation of novel habitats, is one of the defining features of the Anthropocene. Understanding more about the ecological processes that determine the accumulation of native species in novel habitats is essential to better inform conservation efforts, whilst understanding how non-native species associate with novel habitats is vital to prevent the spread of harmful invasive species across the globe. Insects on non-native plants make an ideal model system as non-native

plants are widespread, important ecologically, and may have their distinctiveness captured effectively with a single quantifiable metric (phylogenetic isolation). My work reveals that non-native plants generally host less rich and abundant insect communities than native plants. Insect richness and abundance are lower on phylogenetically isolated non-native plants, and greater on non-native plants with large ranges, and/or an increased time since introduction. Non-native plants, particularly those that are phylogenetically distinctive, are strongly associated with non-native insects, and so may facilitate the spread of invasive species. Importantly, some non-native plants may support native insect biodiversity, as they host similar or even higher levels of insect diversity than native plants, and certain native insect species rely on them in the absence of their original native hosts (particularly within highly modified ecosystems such as gardens). Future research following an insect-plant ecology framework might further investigate the role of insect specialism, the effect of proximity of non-native plants to pools of potential colonists, and the host plant associations of non-native insects in the wider landscape. Additionally, it is important that researchers take a multitrophic insect community approach where possible, with the development of large-scale citizen science projects potentially facilitating this.

From an Anthropocene perspective, my research suggests that novel habitats have a real potential to support native biodiversity in an increasingly altered world, although it is important to bear in mind that many novel habitats may struggle to do so (for example those that are particularly distinctive from pre-existing habitats). Furthermore, novel habitats may facilitate the spread of both invasive and benign species, due to the high association between novel habitats and non-native species. Ultimately, it is vital that we recognise the growing conservation value of both non-native plants and novel habitats, and the array of other ecosystem services that they can provide, whilst simultaneously being cautious of ecosystem disservices.

Appendix 1 Supporting information for Chapter 2

Appendix 1A. List of publications using data from the RHS database

Publications listed in reverse date order (most recent first):

Plant, C.W., Poole, C., Salisbury, A.S. and Bird, S. (2019) The box-tree moth Cydalima perspectalis (Walker, 1859) in Britain: An overview of its spread and current status. *Entomologists Record and Journal of Variation, 131,* 122-147

Tuffen M.G., Salisbury, A. and Malumphy C. (2019) Cotton stringy scale insect, Takahashia japonica Cockerell (Hemiptera: Coccidae), new to Britain. *British Journal of Entomology and Natural History, 32*, 235-241

Bird S. &Salisbury A. (2018) First record of Chrysolina coerulans (Scriba) (Chrysomelidae) in Scotland and further records received by the Royal Horticultural Society (RHS) since 2012. *The Coleopterist, 27*, 123-124

Salisbury, A., Malumphy, C. (2017) Changes in status and distribution of hydrangea scale, Pulvinaria hydrangeae (Hemiptera: Coccidae) in Britain. *British Journal of Entology and Natural History, 30*, 145-153

Salisbury, A. & Jones, P. (2016) The mallow flea beetle, Podagrica fuscicornis (Linnaeus) (Chrysomelidae) – feeding on Honeria and Sidalcea (Malvaceae), new host records. *The Coleopterist 25*, 10

Harris, K.M., Salisbury, A. & Jones, H. (2016) Enigmadiplosis agapanthi, a new genus and species of gall midge (Diptera, Cecidomyiidae) damaging Agapanthus flowers in England. *Cecidology, 31*, 17-20

Malumphy, C. & Salisbury A. (2014) First incursion of Manuka felt scale Acanthococcus mariannae in Britain (Hemiptera: Eriococcidae). *British Journal of Entomology and Natural History, 27*, 21-24

Salisbury, A., Ostoja-Starzewski, J. & Halstead, A.J. (2014) The establishment of Fuchsia gall mite, Aculops fuchsiae Keifer, (Eriophyidae) in England, a serious pest of Fuschia. *British Journal of Entomology and Natural History, 27*, 145-150

Salisbury, A. & Platoni, A. (2013) The green dock beetle, Gastrophysa viridula (De Geer, 1775) (Chrysomelidae); a pest on Begonia (Begoniaceae), a new host record. *The Coleopterist, 22*, 124-125

Salisbury, A., Malumphy, C. & Halstead, A.J. (2013) Euonymus scale Unaspis euonymi (Hemiptera: Diaspididae); an introduced pest of spindle (Euonymus) in Britain. *British Journal of Entomology and Natural History, 26*, 211-217

Salisbury, A. & Halstead, A.J. (2012) Blue mint beetle, Chrysolina coerulans (Scriba) (Chrysomelidae) breeding in Cambridgeshire. *The Coleopterist, 21*:145-146

Salisbury, A., Malumphy, C. & Halstead, A.J. (2012) First record of blue mint beetle Chrysolina coerulans (Scriba) (Chrysomelidae) breeding in Britain. *The Coleopterist. 21*, 35-37

Salisbury, A., Korycinska, A. & Halstead, A.J. (2012) The first occurrence of larvae of the box tree moth, Cydalima perspectalis (Walker, 1859) (Lepidoptera: Crambidae) in private gardens in the UK. *British Journal of Entomology and Natural History, 25*, 1-5

Salisbury, A. & Halstead, A.J. (2011) Galeruca tanaceti (Linnaeus) (Chrysomelidae) a pest on potato foliage (Solanum tuberosum). *The Coleopterist, 20*, 117-118

Malumphy, C., Halstead, A. J. & Salisbury, A. (2011) Changes in distribution and pest status of yew scale, Parthenolecanium pomeranicum (Hemiptera: Coccidae) in Britain between 1944-2010. *British Journal of Entomology and Natural History, 24*, 133-138.

Salisbury, A., Malumphy, C. & Halstead, A.J. (2011) Pittosporum psyllid, Trioza vitreoradiata (Hemiptera: Triozidae) expanding distribution and host range in the UK. *British Journal of Entomology and Natural History, 24*, 69-73

Salisbury, A. & Broad, G. (2011) The hyperparasitoid Mesochorus liliioceriphilus (Hymenoptera: Ichneumonidae), an addition to the parasitoid complex

of the lily beetle, Lilioceris lilii (Coleoptera: Chrysomelidae) in Britain. *British Journal of Entomology and Natural History, 24*, 95-99

Salisbury, A., Halstead, A.J. & Malumphy, C. (2010) Wisteria scale, Eulecanium excrescens (Hemiptera: Coccidae) spreading in south east England. *British Journal of Entomology and Natural History, 23*, 225-228

Salisbury, A., Barclay, M.V.L., Reid, S. & Halstead, A.J. (2009) The current status of the southern green shield bug, Nezara viridula (Hemiptera: Pentatomidae), an introduced pest species recently established in south-east England. *British Journal of Entomology and Natural History, 22*, 189-194

Mabbott, P. & Salisbury, A. (2006) The establishment of the rosemary beetle Chrysolina americana (L.) in London. *The London Naturalist, 85*, 163-166

Mabbott, P. & Salisbury, A. (2005) Bergamont Monarda didyma L. and gentian sage Salvia patens Cavanilles (Lamiaceae) as food plants for Cassida viridis (Linnaeus) (Chrysomelidae). *The Coleopterist. 14*, 38

Salisbury, A. (2004) An additional host plant for Cassida murraea Linnaeus, 1767 (Chrysomelidae: Cassidinae). *The Coleopterist, 13*, 26

Salisbury, A. (2003) A further note on the continued spread in Britain of the Lily Beetle, Lilioceris lilii (Scopoli) (Chrysomelidae), with notes on its host plant range. *The Coleopterist, 12,* 67-75

Salisbury, A. (2003) Further records of Chrysolina americana (Linnaeus) (Chrysomelidae) in Britain. *The Coleopterist, 12*, 61-62

Salisbury, A. (2002) An unusual pabulum for Leptura scutellata (Fabricius, 1781) Coleoptera: Cerambycidae. *The Coleopterist, 11*, 116

Salisbury, A. (2002) The Rosemary Beetle, *Chrysolina americana* (L.) (Col., Chrysomelidae) in Britain. *Entomologists Monthly Magazine, 138*, 77-80

Halstead, A.J. & Salisbury, A. (2002) An additional host for the shoot-cutting weevil Rhynchites germanicus Herbst (Col.: Attelabidae). *Entomologists Record and Journal of Variation, 114*, 179

Table A.1.1 RHS interaction description variables

Variable Name	Definition
ID	Individual record identifier number
RecordNumber	May be used to identify when multiple records originated from the same enquiry
Date	Date of record
Year	Year of record
GridReference	Record location (100 km^2 resolution). Please contact the Royal Horticultural Society (A. Salisbury) for resolutions of up to 1 km^2
Location	Displays general location information for records without grid references. Categories include: -*GridReferenced* = Interaction was grid referenced within Great Britain -*GB* = Interaction recorded in Great Britain or N. Ireland -*Ireland* = Interaction recorded in Ireland -*Non GB* = Interaction recorded overseas -*Uncertain* = No location associated with a record
Sample	Details whether an invertebrate sample was provided for a record. Categories include: -*Illustration* = Illustration of invertebrate provided -*Photo* = Photograph of invertebrate provided -*Sample* = Physical specimen provided -*Not Recorded* = No information regarding sample provision -*No Sample* = Sample not provided
InvertebrateStatus	Invertebrate native status in Great Britain. Assigned to taxa at a species level resolution. Invertebrate native status categories are defined in **Table A1.5**
InvertebrateFeedingType	A broad classification of RHS invertebrate species feeding type. *Herbivore (DBIF)* and *Omnivore (DBIF)* species were assigned feeding types using the DBIF. Feeding types of species not present in the DBIF were determined with a literature search. Categories include: -*Scavenger* = Broad generalist scavengers -*Detritivore* = Feeding on decomposing organic matter -*Herbivore* = Feeding on living plant matter -*Herbivore (DBIF)* = Herbivore listed in the DBIF -*Omnivore* = Feeding on animal and plant matter -*Omnivore (DBIF)* = Omnivore listed in the DBIF -*Parastioid* = Feeding within an invertebrate host -*Predator* = Feeding on animal matter -*Uncertain* = Feeding type indeterminable through literature search -*Not Processed* = Insect taxon at genus level or above

PlantStatus	Plant native status in Great Britain. Assigned to plant taxa at the species level resolution. Plant native status categories are defined in **Table A1.4**
PlantStatusSpecies	Plant native status in Great Britain. Assigned to plant taxa that were 'upgraded' to species level through the removal of subspecies/variety information. Plant native status categories are defined in **Table A1.4**
NeophyteDate	Non-native neophyte plant introduction date to Great Britain. *No Date* = plant species is not classified as a neophyte by Stace & Crawley (2015), and so is without an introduction date. *Not Processed* = plant taxon at genus level or above

A definition of the various interaction description variables in the RHS. Taxonomic description variables are defined in **Table A1.3**.

Table A1.2 DBIF interaction description variables

Variable Name	Definition
ID	Individual record identifier number
Source	The literature source reporting an interaction
SourceID	Unique identifier number for each literature source
SourceYear	The year that each literature source was published
SourceType	A broad classification of a literature source. See **Methods** for a definition of each category. Categories include: *Field Guide, Journal Article*, *Slide Collection*, *Other Article*, *Other Book*, and *Private Article*
SourcePrimarySecondary	Primary or secondary classification of a literature source. Categories include: *Primary* and *Secondary*
InteractionLocationConcat	Concatenation detailing the geographic location of a record as reported by a source. Categories include: *Africa, Asia*, *Europe*, *N. America*, *No Location*, *Other Areas (Non-GB)*
InteractionStatus	A qualitative assessment of the relative importance of a host plant for larval development or adult feeding, as reported in the source literature. Categories include: *Important* and *Not Specified*
RearedCaptive	Details whether an invertebrate-plant interaction emerged from captive rearing. Categories include: *Reared captive* and *Not captive*
LKW	Details the subset of records that were expertly verified by L. Ward, and included in previous analyses. Categories include: *LKW* and *Not LKW*
InvertebrateStatus	Invertebrate native status in Great Britain. Assigned to taxa at a species level resolution. Invertebrate native status categories are defined in **Table A1.5**
InvertebrateStatusSpecies	Invertebrate native status in Great Britain. Assigned to invertebrate taxa that were 'upgraded' to species level through the removal of subspecies/variety information. Invertebrate native status categories are defined in **Table A1.5**
FeedingPhytophagous	Details whether a source reported an invertebrate-plant interaction as phytophagous. Categories include: *Phytophagous* and *Not Phytophagous*
FeedingAllConcat	Concatenation of various feeding types/behaviours associated with an invertebrate-plant interaction. Feeding type categories are defined in **Table A1.6**
InvertebrateStageConcat	Concatenation reporting the invertebrate life stage(s) associated with an interaction. Categories include: *Adults*, *Adults + Larvae*, *Larvae*, *Oviposition*, *Pupa*, and *Unspecified*

MonthsAdultConcat	Concatenation detailing the months(s) that an invertebrate is in the adult stage
MonthsImmatureConcat	Concatenation detailing the months(s) that an invertebrate is in an immature stage
HostPartsConcat	Concatenation detailing host part usage as reported by a source. Categories include: *Bark, Wood, Roots, Microflora, Bulbs, Dead parts, Branch (large), Branch (small), Stumps, Other part, Exudations, Litter, Trunk, Rhizomes, Fruits/seeds, Pollen/nectar, Flowers, Shoots, Flower buds, Vegetative buds, Leaves,* and *Stems*
PestStatus	Details if a source reported an invertebrate as a pest. Categories include: *Pest* and *Not Specified*
PlantStatus	Plant native status in Great Britain. Assigned to plant taxa at the species level resolution. Plant native status categories are defined in **Table A1.4**
PlantStatusSpecies	Plant native status in Great Britain. Assigned to plant taxa that were 'upgraded' to species level through the removal of subspecies/variety information. Plant native status categories are defined in **Table A1.4**
NeophyteDate	Non-native neophyte plant introduction date to Great Britain. *No Date* = plant species is not classified as a neophyte by Stace & Crawley (2015), and so is without an introduction date. *Not Processed* = plant taxon at genus level or above

A definition of the various interaction description variables in the DBIF. Taxonomic description variables are defined in **Table A1.3**.

Table A1.3 RHS and DBIF taxonomic description variables

Variable Name(s)	Definition
InvertebrateTaxa/PlantTaxa	Invertebrate/plant taxon name
InvertebrateFamily/PlantFamily	Invertebrate/plant family name
InvertebrateOrder/PlantOrder	Invertebrate/plant order name
InvertebrateHigherClass/ PlantHigherClass	Invertebrate/plant higher taxonomic classification (e.g. Plants = Angiosperm, Bryophyte, Gymnosperm, etc.; Insects = Acari, Annelida, Arachnida, etc.)
InvertebrateLevel/PlantLevel	Invertebrate/plant taxon resolution. Taxa were identified to as close to species level as possible with the information provided by RHS members and DBIF source literature
InvertebrateNameOriginator/PlantNameOriginator	Invertebrate/plant name originator. Provided where available. If names were not listed within any sources this variable is blank
InvertebrateUKSI/PlantUKSI	Invertebrate/plant United Kingdom Species Inventory identifier code. Invertebrates and plants not found in the UKSI are marked as *MissingInsect* or *MissingPlant*

A definition of the taxonomic variables in the RHS and the DBIF. Interaction description variables are defined in **Tables A1.1 and A1.2**.

Table A1.4 RHS and DBIF plant native statuses

Native Status	Definition
Not Found	Plant not found in any source
Not Processed	Plant at genus level or higher, and so not assigned a native status
Matched to Full Taxon	"PlantStatusSpecies" column only: Native status matched to plant with full taxonomic information (including subspecies and varieties)
Trimmed to Species	"PlantStatus" column only: Native status matched to plant after it was 'upgraded' to the species level (removal of subspecies and varieties)
S&C Neophyte	Non-native neophyte – determined by Stace & Crawley (2015)
S&C Archaeophyte	Non-native archaeophyte – determined by Stace & Crawley (2015)
S&C Uncertain	Uncertain native/non-native – determined by Stace & Crawley (2015)
Stace3 Native	Native – determined by Stace's "*New Flora of the British Isles*" (2010)
PlantAtt Native	Native – determined by PlantAtt (Hill et al. 2004)
PlantAtt Neophyte	Non-native neophyte – determined by PlantAtt (Hill et al. 2004)
PlantAtt Archaeophyte	Non-native archaeophyte – determined by PlantAtt (Hill et al. 2004)
PlantAtt Uncertain	Uncertain native/non-native – as determined by PlantAtt (Hill et al. 2004)
Kew Native	Native – determined from native range as listed by Kew POWO (2019)
Kew Neophyte	Non-native neophyte – determined from native range as listed by Kew POWO (2019)
Kew Non-Native	Non-native of uncertain neophyte/archaeophyte status – determined from native range as listed by Kew POWO (2019)
Kew No Data	Uncertain native/non-native – no native range listed by Kew POWO (2019)

A definition of the various plant native statuses associated with records in the RHS and the DBIF. The 'PlantStatus' column reports the above native statuses matched to plants with full taxonomic information (including subspecies and varieties). The 'PlantStatusSpecies' column reports native statuses matched to plants after they were 'upgraded' to the species level (removal of subspecies and variety information). See **Methods** for further details of the plant native status matching process. See **Fig. 2.3** for a breakdown of plant native status proportions in the DBIF and RHS.

Table A1.5 RHS and DBIF invertebrate native statuses

Native status	Definition
Not Found	Invertebrate not found in any source
Not Processed	Invertebrate at genus level or higher, and so not assigned a native status
Matched to Full Taxon	"InvertebrateStatusSpecies" column only: Native status matched to invertebrate with full taxonomic information (including subspecies)
Trimmed to Species	"InvertebrateStatus" column only: Native status matched to invertebrate after it was 'upgraded' to the species level (removal of subspecies)
Native	Native – determined by matching with the United Kingdom Species Inventory (UKSI) following the removal of the non-native invertebrates listed in the GBNNSIP (NNSS 2019)
Probably Native	Native status as listed in the GBNNSIP (NNSS 2019)
Probably Non-Native	Native status as listed in the GBNNSIP (NNSS 2019)
Dependent Non-Native	Native status as listed in the GBNNSIP (NNSS 2019)
New Arrival	Native status as listed in the GBNNSIP (NNSS 2019)
Non-Native	Native status as listed in the GBNNSIP (NNSS 2019)
Not Yet Assigned	Native status as listed in the GBNNSIP (NNSS 2019)
Unknown	Native status as listed in the GBNNSIP (NNSS 2019)

A definition of the various invertebrate native statuses associated with records in the RHS and the DBIF. The 'InvertebrateStatus' column reports the above native statuses matched to invertebrates with full taxonomic information (including subspecies). The 'InvertebrateStatusSpecies' column reports native statuses matched to invertebrates after they were 'upgraded' to the species level (removal of subspecies). 'InvertebrateStatusSpecies' was present only within the DBIF, as all invertebrate taxa at the species level in the RHS were matched with a status using all available subspecies/variety information where available. See **Methods** for further details of the invertebrate native status matching process. See **Fig. 2.3** for a breakdown of invertebrate native statuses proportions in the DBIF and RHS.

Table A1.6 DBIF interaction feeding types/behaviours

Feeding type/behaviour	Definition
Gregarious	Individuals feeding in groups
Sheltering	Plant being used for shelter
Symbiotic	A symbiotic interaction
Associated	Interaction is not a herbivore on a host plant, but a close linkage exists, e.g. ants attending a host or an inquiline in a gall. Usually entered with the addition of more specific categories
Ant attended	Herbivore on a host in association with ants
Myrmecophile	Herbivore on a host in close association with ants
Predacious	Feeding on animal matter (but the invertebrate in close association with a herbivore or plant host)
Partly predacious	Feeding partly on animal matter
Parasitic	Parasitizing an invertebrate host (an invertebrate is classified as a parasitoid if it kills the host as part of its life-cycle)
Omnivorous	Feeding on plant and animal matter
Saprophagous	Feeding on decaying organic matter
Fungivorous	Feeding on Fungi
Other phagy	An unusual type of phagy not included in the other categories
Polyphagous	Source reports 'polyphagous' or text to the effect of 'many other plants'. If listed without the 'Phytophagous' category the source did not report an herbivorous interaction, but reported the invertebrate as feeding on other plants.
Phytophagous	Entered for all herbivorous interactions
Mining	Specific type of phytophagy
Galling	Specific type of phytophagy
Grazing	Specific type of phytophagy
Boring	Specific type of phytophagy
Rolling	Specific type of phytophagy
Skeletonizing	Specific type of phytophagy

Webbing	Specific type of phytophagy
Inquiline	Feeding within a structure (usually a gall) created by another herbivore

A definition of the various feeding types/behaviours associated with records in the DBIF, as reported in the 'FeedingAllConcat' column.

Appendix 2 Supporting information for Chapter 3

Appendix 2A. Local-scale plant mixtures

Each mixture of plants contained 14 species, as detailed in **Table A2.1**, and each plant species was planted in a standardized position within its plot (**Fig. A2.1**). The positions of the plots on the two experimental sites are shown in **Fig. A2.2**.

Table A2.1 Plant species in each species group and native status on the local-scale plots

Position in Plot	Native	Congener	Exotic	Triplet Included in Vortis Analysis	Triplet Included in Pollinator Analysis
Species group A					
1	*Lonicera periclymenum* 'Graham Thomas'	*Lonicera tragophylla* *1*	*Eccremocarpus scaber*	Just N and C	Yes
2	*Primula vulgaris*	*Primula japonica* 'Miller's Crimson'	*Oxalis adenophylla*	No	Yes
3	*Hyacinthoides non-scripta*	*Hyacinthoides hispanica* *2*	*Nerine bowdenii* or *Ornithogalum candicans* *3*	Just E	Yes
4	*Valeriana officinalis*	*Valeriana phu* 'Aurea'	*Diascia personata* 'Hopleys'*4*	Yes	Yes
5	*Deschampsia cespitosa*	*Stipa tenuissima*	*Uncinia rubra* Colenso *6*	Yes	No
6	*Buxus sempervirens*	*Sarcococca hookeriana* var. *humilis*	*Pittosporum tenuifolium*	Yes	Yes
7	*Viburnum opulus*	*Viburnum sargentii*	*Ozothamnus rosmarinifolius* or *Azara serrata* *5*	Just E	Yes
8	*Lythrum salicaria*	*Lythrum virgatum* 'Dropmore Purple'	*Mirabilis jalapa* *4*	Yes	Yes
9	*Cytisus scoparius*	*Genista lydia* Boiss.	*Callistemon rigidus**	No	Yes
10	*Geranium sanguineum*	*Geranium macrorrhizum*	*Leptinella squalida* 'Platt's Black'	Yes	Yes
11	*Stachys officinalis*	*Stachys byzantina*	*Lobelia tupa* *4*	Yes	Yes
12	*Armeria maritima*	*Armeria juniperifolia*	*Sisyrinchium striatum* Sm.	Yes	Yes
13	*Scabiosa columbaria*	*Scabiosa caucasica*	*Eryngium agavifolium*	No	Yes
14	*Leucanthemum vulgare* (Vail)	*Rhodanthemum hosmariense* or *Anthemis punctata* *7*	*Euryops pectinatus* or *Euryops tysonii* *6*,*8*	Yes	Yes
Species group B					
1	*Lonicera periclymenum* 'Graham Thomas'	*Lonicera tragophylla* *1*	*Eccremocarpus scaber*	Just N and C	Yes
2	*Dianthus deltoides*	*Dianthus plumarius*	*Acaena microphylla*	Yes	Yes
3	*Primula vulgaris*	*Primula japonica* 'Miller's Crimson'	*Oxalis adenophylla*	No	Yes

4	*Eupatorium cannabinum*	*Eupatorium maculatum* 'Orchard Dene'	*Verbena bonariensis*	No	Yes
5	*Dryopteris filix-mas* Schott	*Dryopteris wallichiana*	*Polystichum proliferum*	No	No
6	*Buxus sempervirens*	*Sarcococca hookeriana* var. *humilis*	*Pittosporum tenuifolium*	Yes	Yes
7	*Rosa rubiginosa*	*Rosa glauca*	*Fuchsia magellanica* var. *gracilis*	Just N and E	Yes
8	*Lythrum salicaria*	*Lythrum virgatum* 'Dropmore Purple'	*Mirabilis jalapa* *4*	Yes	Yes
9	*Cytisus scoparius*	*Genista lydia*	*Callistemon rigidus**	No	Yes
10	*Geranium sanguineum*	*Geranium macrorrhizum*	*Leptinella squalida* 'Platt's Black'	Yes	Yes
11	*Knautia arvensis*	*Knautia macedonica*	*Alstroemeria psittacina*	Yes	Yes
12	*Armeria maritima*	*Armeria juniperifolia*	*Sisyrinchium striatum*	Yes	Yes
13	*Malva moschata* or *Silene uniflora* *9*	*Malva alcea* or *Lychnis flos-jovis* *10*	*Osteospermum jucundum*	Yes	Yes
14	*Leucanthemum vulgare*	*Rhodanthemum hosmariense* or *Anthemis punctata* *7*	*Euryops pectinatus* or *Euryops tysonii* *6*,*8*	Yes	Yes
Species group C					
1	*Lonicera periclymenum* 'Graham Thomas'	*Lonicera tragophylla* *1*	*Eccremocarpus scaber*	Just N and C	Yes
2	*Dianthus deltoides*	*Dianthus plumarius*	*Acaena microphylla*	Yes	Yes
3	*Hyacinthoides non-scripta* *2*	*Hyacinthoides hispanica* *2*	*Nerine bowdenii* or *Ornithogalum candicans* *3*	Just E	Yes
4	*Eupatorium cannabinum*	*Eupatorium maculatum* 'Orchard Dene'	*Verbena bonariensis*	No	Yes
5	*Molinia caerulea* Moench	*Calamagrostis brachytricha*	*Carex testacea*	Yes	Just N
6	*Buxus sempervirens*	*Sarcococca hookeriana* var. *humilis*	*Pittosporum tenuifolium*	Yes	Yes
7	*Rosa rubiginosa*	*Rosa glauca*	*Fuchsia magellanica* var. *gracilis*	Just N and E	Yes
8	*Veronica spicata*	*Veronica austriaca* subsp. *teucrium*	*Hebe rakaiensis*	No	Yes

9	*Malva moschata* or *Silene uniflora* *9*	*Malva alcea* or *Lychnis flos-jovis* *10*	*Osteospermum jucundum*	Yes	Yes
10	*Helianthemum nummularium*	*Halimium umbellatum*	*Brachyglottis monroi*	No	Yes
11	*Stachys officinalis*	*Stachys byzantina*	*Lobelia tupa* *4*	Yes	Yes
12	*Armeria maritima*	*Armeria juniperifolia*	*Sisyrinchium striatum*	Yes	Yes
13	*Scabiosa columbaria*	*Scabiosa caucasica*	*Eryngium agavifolium*	No	Yes
14	*Leucanthemum vulgare*	*Rhodanthemum hosmariense* or *Anthemis punctata* *7*	*Euryops pectinatus* or *Euryops tysonii* *6*,*8*	Yes	Yes

1 Incorrect species supplied – replaced with correct species spring 2011
2 Incorrect species supplied – replaced with correct species in summer 2010
3 Original *Nerine bowdenii* (pollinator sampling) replaced by *Ornithogalum candicans* in spring 2015 (Vortis sampling)
4 Plants replaced by the same species due to winter losses in 2010/11
5 Original *Ozothamnus rosmarinifolius* (pollinator sampling) died due to *Phytophora* root rot – replaced spring 2011, by *Azara serrata* (pollinator and Vortis sampling)
6 Plants replaced by the same species due to winter losses in 2011/12
7 Original *Rhodanthemum hosmariense* (pollinator sampling) replaced by *Anthemis punctata* in spring 2015 (Vortis sampling)
8 Replaced *Euryops pectinatus* (pollinator sampling), which was lost in winter 2010/11, by *Euryops tysonii* (pollinator and Vortis sampling)
9 Original *Malva moschata* (pollinators) replaced in spring 2015 by *Silene uniflora* (Vortis sampling)
10 Original *Malva alcea* (pollinators) replaced by *Lychnis flos-jovis* in spring 2015 (Vortis sampling)

Adapted from table previously published in supplementary information with Salisbury et al. 2015. Not all plant species were included in each analysis. Criteria for inclusion are detailed in main text. For a full list of all plant species with associated plant traits and insect diversity see raw data in *Wisley Experimental Data.xlsx*. In three cases exotic plants were part of the same family as the native plant in their species triplet. These were *Euryops tysonii* (Asteraceae - grouped with *Leucanthemum vulgare*), *Hebe rakaiensis* (Plantaginaceae – grouped with *Veronica spicata*), and Polystichum proliferum (Dryopteridaceae – grouped with *Dryopteris filix-mas*). In all other cases exotics were more distantly related. N = native, C = congener, E = exotic. The species mixtures referred to in the main text consist of the 14 native species in group A (the first mixture), the 14 congener species in group A (the second mixture), and so on, through to the 14 exotic species in group C (the ninth mixture). The numbers (first column) refer to the position that each plant species was planted in each plot (Fig. A2.1) of a given mixture type, and each row in the table connects a given species triplet.

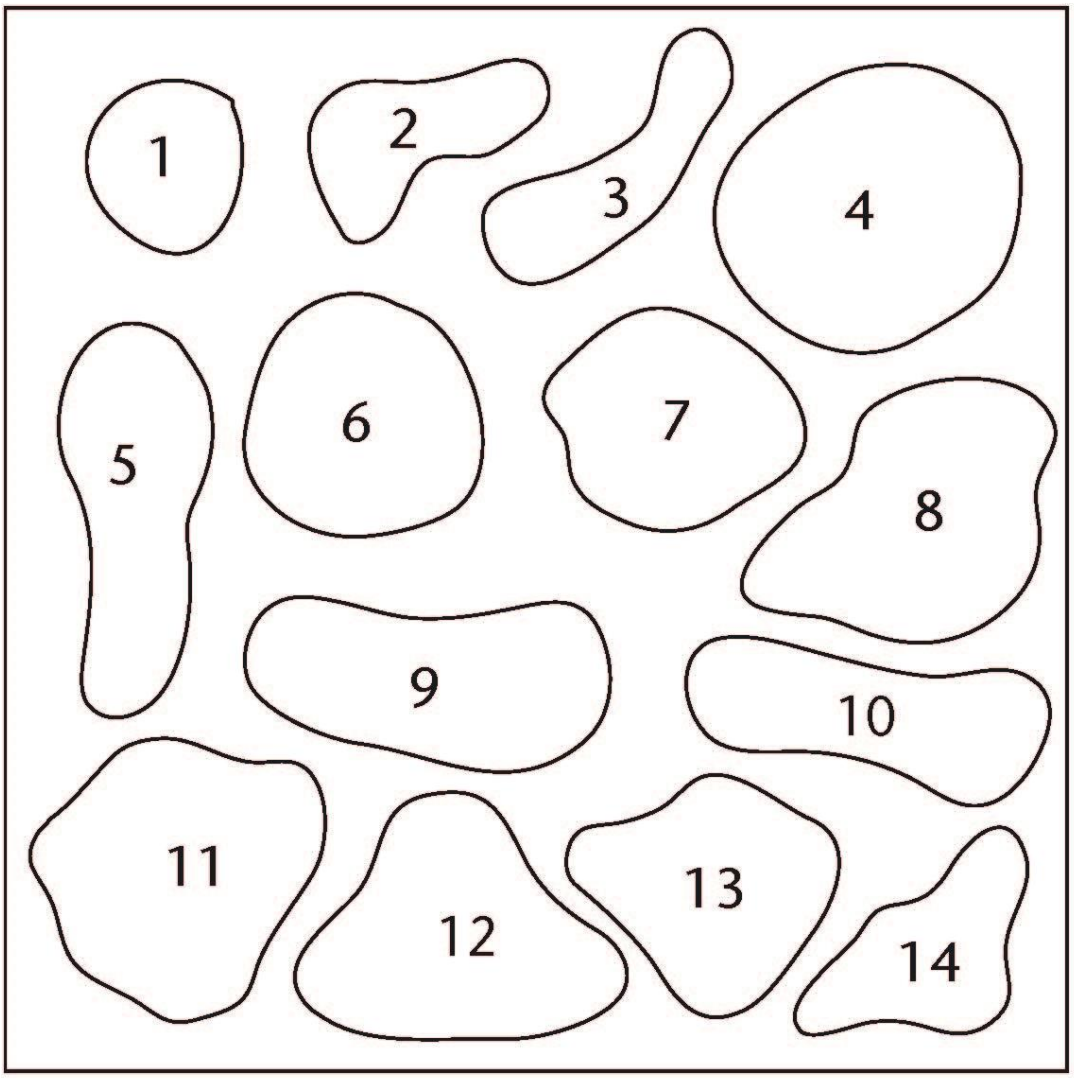

Figure A2.1: Local-scale experimental planting plan. Adapted from figure previously published in supplementary information with Salisbury et al. 2015. The layout of plant species within each 3 x 3m plot followed a standardized pattern. Within each plot the plant species labels represent the following: 1, Climber; 2, Perennial (deciduous or groundcover); 3, Perennial (deciduous or bulbous); 4, Perennial (deciduous); 5, Perennial (grass/grass-like plant or fern); 6, Shrub; 7, Shrub; 8, Shrub or perennial (deciduous); 9, Shrub or perennial (deciduous); 10, Low growing shrub or perennial (deciduous); 11, Perennial (deciduous); 12, Perennial (evergreen); 13, Perennial (deciduous); 14, Low shrub or perennial (deciduous). Note that the term 'perennial' is used here in its horticultural meaning as a noun (i.e. a non-woody plant that lives for multiple years) not an adjective (i.e. a descriptive term for any plant that lives for multiple years).

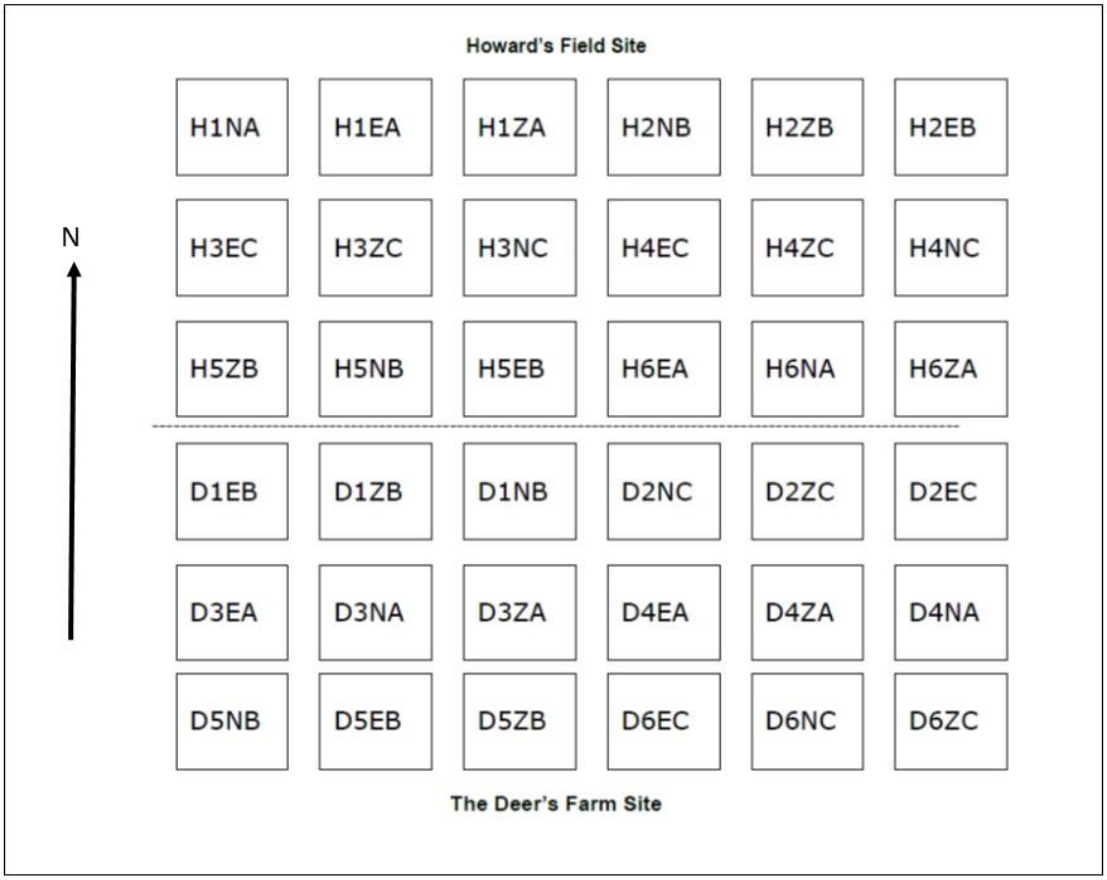

Figure A2.2: Local-scale experimental plot layout. Adapted from figure previously published in supplementary information with Salisbury et al. 2017. H = Site 1 (Howard's Field), D= Site 2 (Deer's Farm). 1 – 6 represent triplet organisation at each site. N = Native Plants, Z = Congener Plants, E = Exotic Plants. A, B, C = Plant Group (See Table A2.1).

Appendix 2B. Local-scale protocols for horticultural management practice

Initial planting took place between May 2009 and June 2010, and subsequent management followed the protocols of Salisbury et al. (2015). In summary:

Weed control: All plants not intentionally planted were hand weeded to prevent competition with the plant assemblages and the provision of resources that could potentially be used by insects. Self-sown seedlings of plants within the planting scheme were also removed unless required to fill gaps of that plant within its allotted space.

Pesticides: No pesticides were used.

Plant restriction, support and pruning: Plants were allowed to flourish within the area defined by the planting plan (**Fig. A2.1**). Any plant material that overhung the edge of a plot to the extent that it touched the ground, reached a height above 2.4 m or had encroached beyond its allotted space within a plot was restricted, by pruning, staking or removal. Pruning to restrict growth was carried out in such a way as to minimize loss of flowers and/or seed-heads. Plants were not deadheaded ('removal of dead and dying flowers') as any seed/fruit set would be lost with potential effects on insects associated with that resource. Dead stems of herbaceous perennials were left standing through winter and cut back in February, conforming to 'wildlife-friendly' gardening advice (Baines, 2000).

Irrigation**:** Watering was carried out as required to enable plant establishment, and to ensure plant survival during drought conditions (e.g. summer 2013).

Winter protection: From 2012/13 onwards, a dry mulch of straw was applied to protect a number of plants that had been lost in preceding winters.

Plant replacement: Occasional plant failures (e.g. because of winter losses, disease, or turnover in short-lived perennials) were normally replaced by the same species (and cultivar). In some instances, alternative plants cultivars/species were used, as detailed in **Table A2.1**.

Appendix 2C. Local-scale pollinator sampling protocol

Recording occurred between May and September when temperatures were greater than 17 °C, wind speeds were less than 5 on the Beaufort scale, and it was neither raining nor likely to rain. In March and April recording took place when temperatures were greater than 8 °C, it was not raining, cloud cover was less than 25%, and wind speed was less than 2 on the Beaufort scale. To minimise the effects of possible diurnal variation in insect visits, each plot was visited twice on each sampling day. Morning sampling sessions started between 09:00 and 10:00, and afternoon sampling sessions between 13:00 and 14:00. Consequently, each plot was sampled for eight minutes on each sampling day. The two experimental sites were visited on different days, with sampling of the second site always occurring within seven days of the first. The order of visiting each plot type (plant mixture) was randomised prior to each recording event.

Appendix 2D. Local-scale Vortis sampling protocol

Vortis sampling occurred after 10:00, when vegetation was dry to the touch, and with temperatures greater than 17°C. The two experimental sites were sampled alternately, with sampling sessions rotating between them. Vortis sampling was carried out by sweeping the suction nozzle across half of each individual plant for 30 seconds. From ground level the Vortis was moved in a sweeping motion up the plant (ensuring not to touch the ground to avoid accidental sampling of soil invertebrates), terminating at the top of the plant, or otherwise at a height of 1.5 metres. To provide consistency, R. Padovani carried out all Vortis sampling. After sampling each plant, the collection tube was removed, stored in a cool box in the field, then sorted using a pooter in the laboratory to separate insects from plant debris (after being stored at 4-10 °C for ~20 minutes to reduce insect activity). Insects were then frozen and stored at -20 °C until identification.

Appendix 2E. Local-scale Vortis plant architecture methods

Plant Area: Overhead photographs (Sony Cyber-shot DSC- HX1 camera) were taken of each plot from a 3.6 m tripod ladder (Niwaki, Somerset, UK), with a 1 m rule placed in shot as a reference. If a plant was obscured from the overhead perspective by another plant, photographs were taken from the side of each bed, whilst holding the camera as high as possible over the plant in question, in order to retain a near-vertical position over the plant. The area of each plant was then measured using the program ImageJ (Schneider, Rasband, & Eliceiri, 2012). Some plants were obscured from overhead photographs and too tall for manual photographs. In these cases, estimates of area were taken through

direct measurement with a rule of the length and width of each plant along two perpendicular axes. The height of each plant was multiplied by its area, to give an overall index of volume for inclusion in the analyses.

Branching Architecture: The branching architecture (apical dominance index) of each plant species was taken to be the number of (living/with leaves) divisions along each branch, divided by the length of branch. The length of a branch was the distance (cm) from the tip of a terminal, leaf-bearing branch, down the stem until we encountered a dead (leafless) sub-branch. This was measured for three branches on the median height individual of each plant species, and the average taken.

Appendix 2F. R packages used for analysis

A list of R packages used for various functions is as follows: data manipulation = reshape (Wickham, 2007), plyr (Wickham, 2011), stringr (Wickham, 2017), and data.table (Dowle & Srinivasan, 2017); Chao-Sorensen dissimilarity index = CommEcol (Melo, 2017); NMDS analysis = vegan (Oksanen et al., 2018); d' specialisation index calculation = bipartite (Dormann, Gruber, & Fruend, 2008); sample based rarefaction = iNEXT (Hsieh, Ma, & Chao, 2016); D^2 calculation = modEvA (Barbosa, Brown, Jimenez-Valverde, & Real, 2016); likelihood ratio tests = lmtest (Zeileis & Hothorn, 2002); negative binomial models = MASS (Venables & Ripley, 2002); beta models = betreg (Cribari-Neto & Zeileis, 2010); type II deviance calculation = car (Fox & Weisberg, 2019); post-hoc Tukey contrasts = multcomp (Hothorn, Bretz, & Westfall, 2008); figures = ggplot2 (Wickham, 2009); adding significance

bars to box plots = ggsignif (Ahlmann-Eltze, 2017); beta regression figures = sjPlot (Lüdecke, 2019); Venn diagrams = limma (Ritchie et al., 2015).

Appendix 2G. Predictor cross-correlation analysis

We examined correlations among all predictor variables which were candidates for inclusion in models.

Local-scale: The effect of host plant native status (native, congener, exotic) on all other pollinator and Vortis model predictors was examined using Kruskal-Wallis tests. The only significant effect of status (other than those shown in the main results) was on pollinator host plant median Julian date ($\chi 2 = 9.21$, $p = 0.010$, d.f. = 2). However, this predictor did not significantly improve the overall pollinator models, and so was not included in the final analysis. All other continuous pollinator and Vortis model predictors were tested for correlation with each other using Kendall Tau-b correlation. No significant correlations existed between Vortis predictors included in the models for final analysis. There were several correlations between pollinator model phylogenetic predictors (mean phylogenetic isolation, nearest phylogenetic neighbour distance, and non-native host plant mean phylogenetic isolation from natives) and the number of host plant replicates, but these were weak (tau = -0.238, -0.229, -0.244), and were therefore unlikely to have impacted our analyses.

Geographic-scale: Host plant native status (native, archaeophyte, neophyte) was significantly or marginally ($0.05 < p < 0.1$) associated with all DBIF model predictors (i.e.

sources Kruskal-Wallis $\chi2 = 68.70$, $p < 1e\text{-}04$, d.f. = 2; hectads $\chi2 = 185.00$, $p < 1e\text{-}04$, d.f. = 2; mean phylogenetic isolation $\chi2 = 8.76$, $p = 0.013$, d.f. = 2; nearest phylogenetic neighbour distance $\chi2 = 26.81$, $p < 1e\text{-}04$, d.f. = 2; non-native host plant mean phylogenetic isolation from natives $\chi2 = 3.70$, $p = 0.054$, d.f. = 1; non-native host plant nearest native phylogenetic neighbour distance $\chi2 = 30.74$, $p < 1e\text{-}04$, d.f. = 1). This may explain the loss of significance of two of our four metrics of phylogenetic isolation when included in the same model as host plant native status (**Table A2.6**).

Sampling effort (the number of separate sources in the DBIF database reporting insects associated with a particular plant species) was correlated with non-native host plant mean phylogenetic isolation from natives, host plant range size (hectads) and neophyte introduction date, however the correlations were weak (Kendall Tau-b correlation tau = 0.08, 0.38 and 0.14, respectively), and were therefore unlikely to have impacted our analyses. Host plant range size (hectads) and neophyte introduction date were also weakly correlated (tau = 0.23).

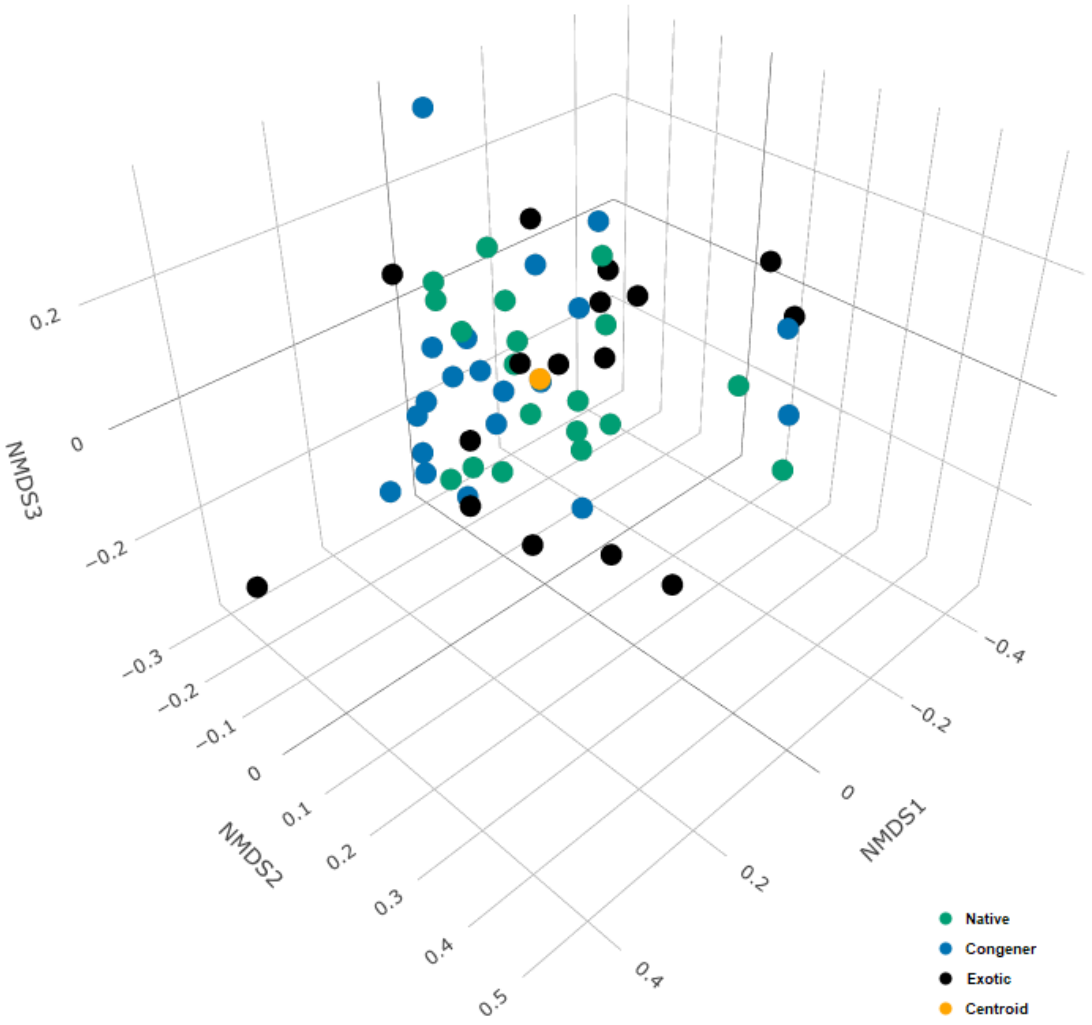

Figure A2.3: Three-dimensional non-metric multidimensional scaling (NMDS) of Chao-Sorensen abundance-based dissimilarities of local-scale pollinator communities. Stress = 0.165, indicating a good representation of the data in the reduced dimensions. Each point represents a plant species. The distance from each point to the group centroid (0, 0, 0) represents the distinctiveness of the insect community on that plant species.

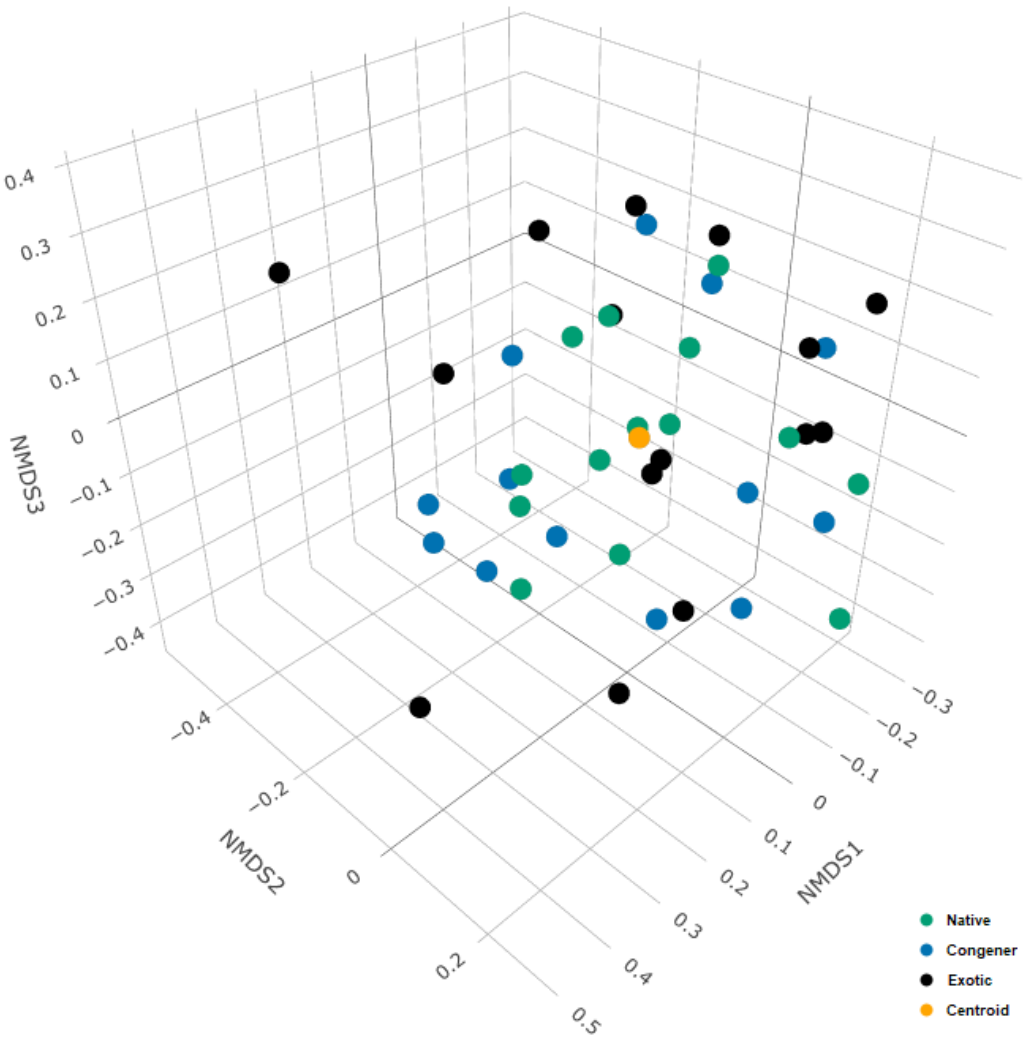

Figure A2.4: Three-dimensional non-metric multidimensional scaling (NMDS) of Chao-Sorensen abundance-based dissimilarities of local-scale Vortis insect communities. Stress = 0.161, indicating a good representation of the data in the reduced dimensions. Each point represents a plant species. The distance from each point to the group centroid (0, 0, 0) represents the distinctiveness of the insect community on that plant species.

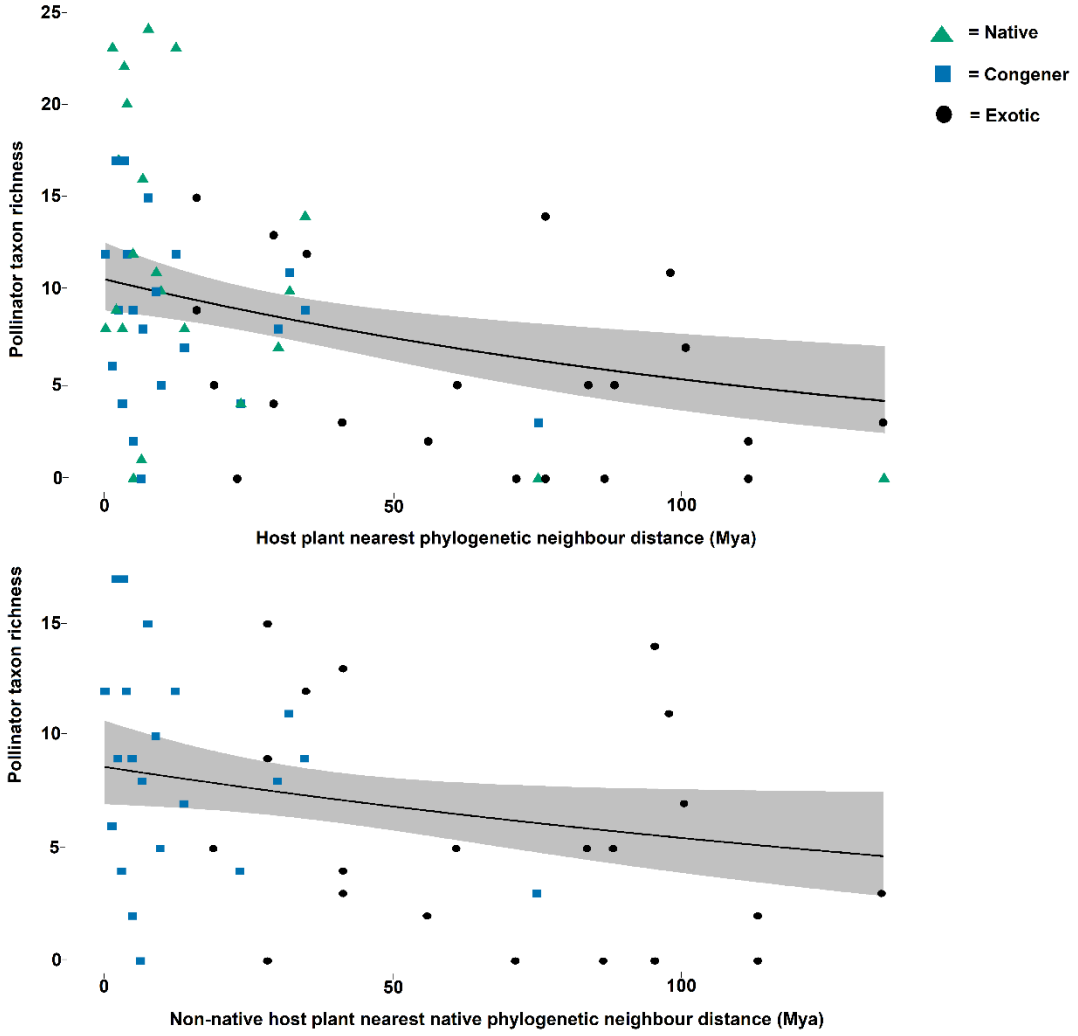

Figure A2.5: The effect of host plant phylogenetic isolation on local-scale pollinator abundance and taxon richness. Partial regression plots display the effect of our focal predictor (phylogenetic isolation), whilst holding all other predictors at their mean. Shaded areas represent 95% confidence intervals. Data points represent individual plants species. Nearest phylogenetic neighbour distance (NPN) = distance in millions of years from host plant to closest phylogenetic neighbour in the local community. Non-native host plant nearest native phylogenetic neighbour distance (NPNN) = distance in millions of years from *non-native* host plant to closest *native* phylogenetic neighbour in the local community. See Methods for details of the calculation of D^2 and D.

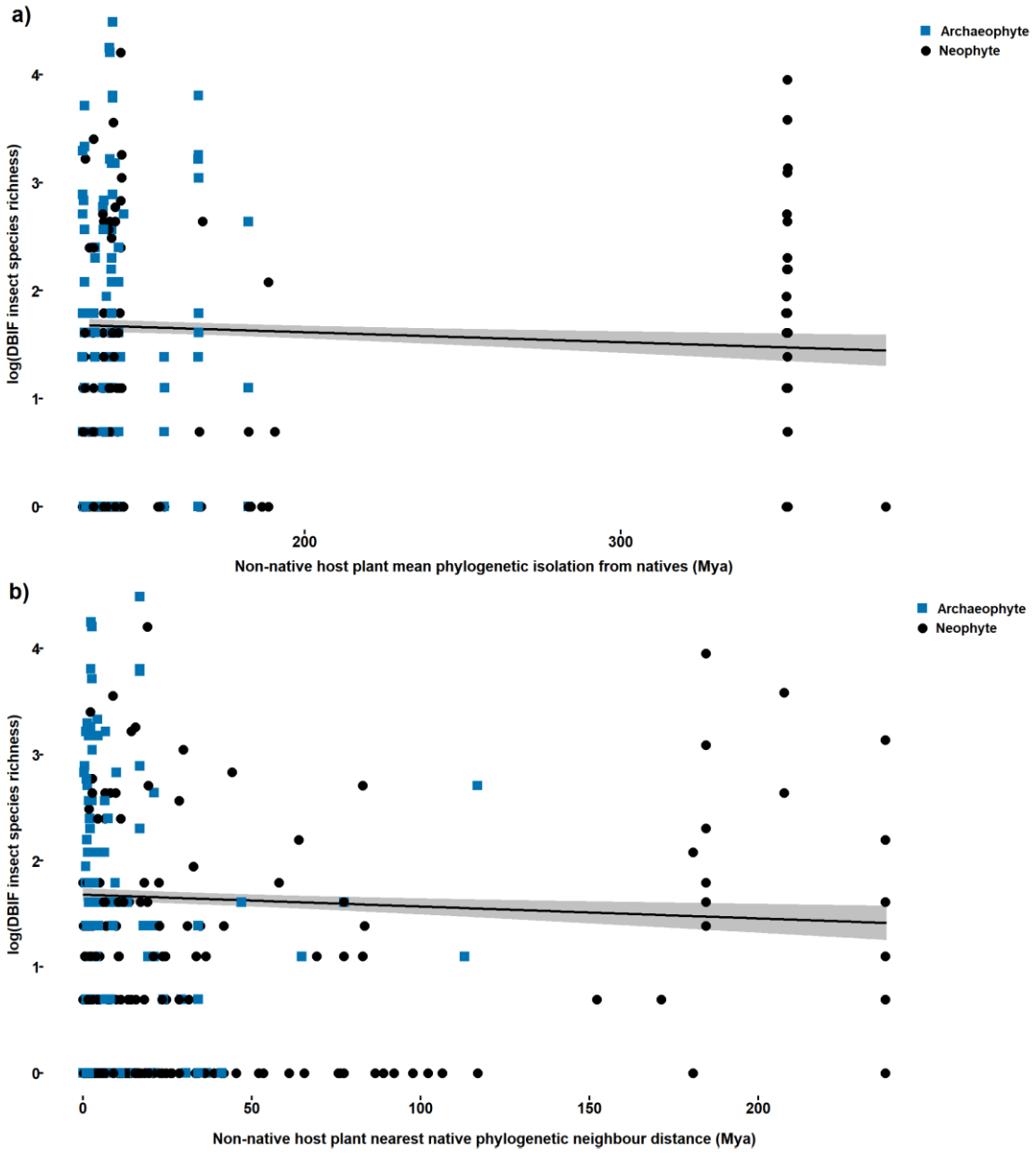

Figure A2.6: The effect of phylogenetic isolation on geographic-scale DBIF insect species richness. Partial regression plots display the effect of our focal predictor (phylogenetic isolation), whilst holding all other predictors at their mean. Shaded areas represent 95% confidence intervals. Data points represent individual plants species. Non-native host plant mean phylogenetic isolation from natives (PIN) = mean distance in millions of years from *non-native* host plant to all other *native* plants in the DBIF. Non-native host plant nearest native phylogenetic neighbour distance (NPNN) = distance in millions of years from *non-native* host plant to closest *native* phylogenetic neighbour in the DBIF. See Methods for details of the calculation of D^2 and D.

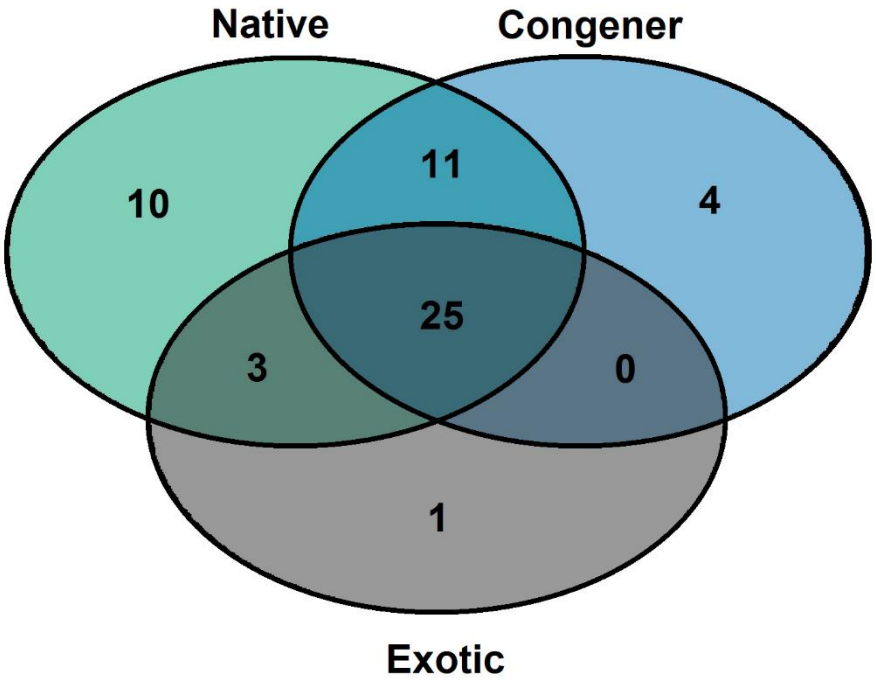

Figure A2.7: Venn diagram displaying the number of local-scale pollinators unique to, and shared between each host plant native status. Sample size of Native = 23 plant species, Congener = 21, Exotic = 20.

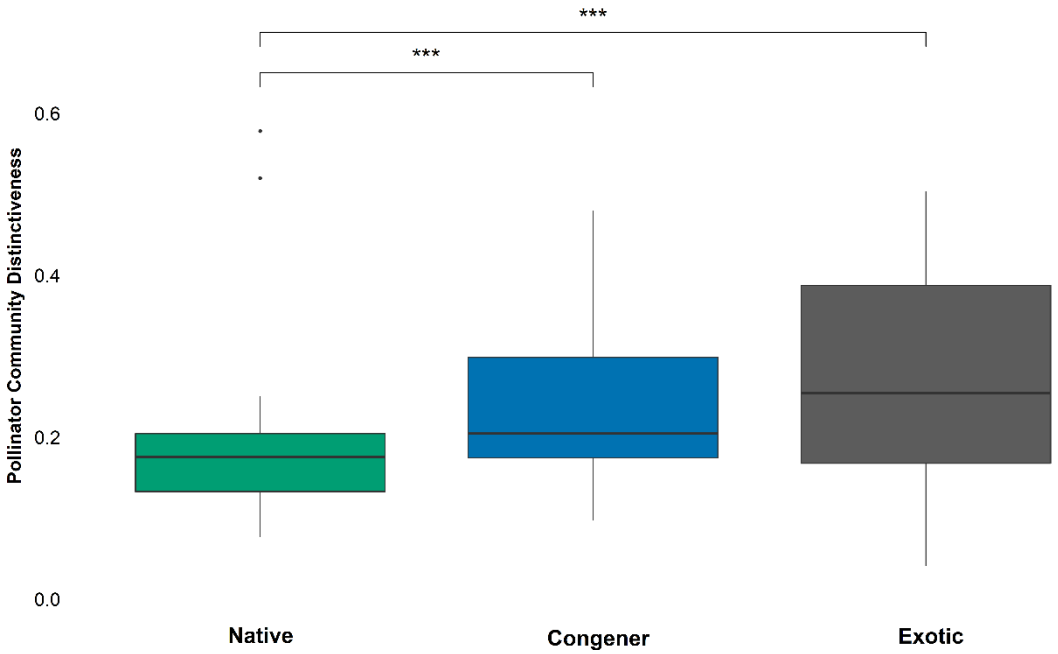

Figure A2.8: Local-scale pollinator insect community distinctiveness on the different host plant statuses. Pollinator insect distinctiveness was calculated using a non-metric multidimensional scaling approach (see Methods). Boxplots represent median, interquartile range, and 1.5x the interquartile range. Boxplot points represent outliers. *** = significance of Tukey post-hoc contrasts < 0.001. Beta model (Pollinator Insect Community Distinctiveness ~ log(Replicates) + Flowering Units + Status | Status + Median Julian Sampling Date) pseudo R^2 = 0.235. Sample size of Native = 19 plant species, Congeneric = 20, Exotic = 16. See Methods for the distinction between beta regression mean and precision submodels.

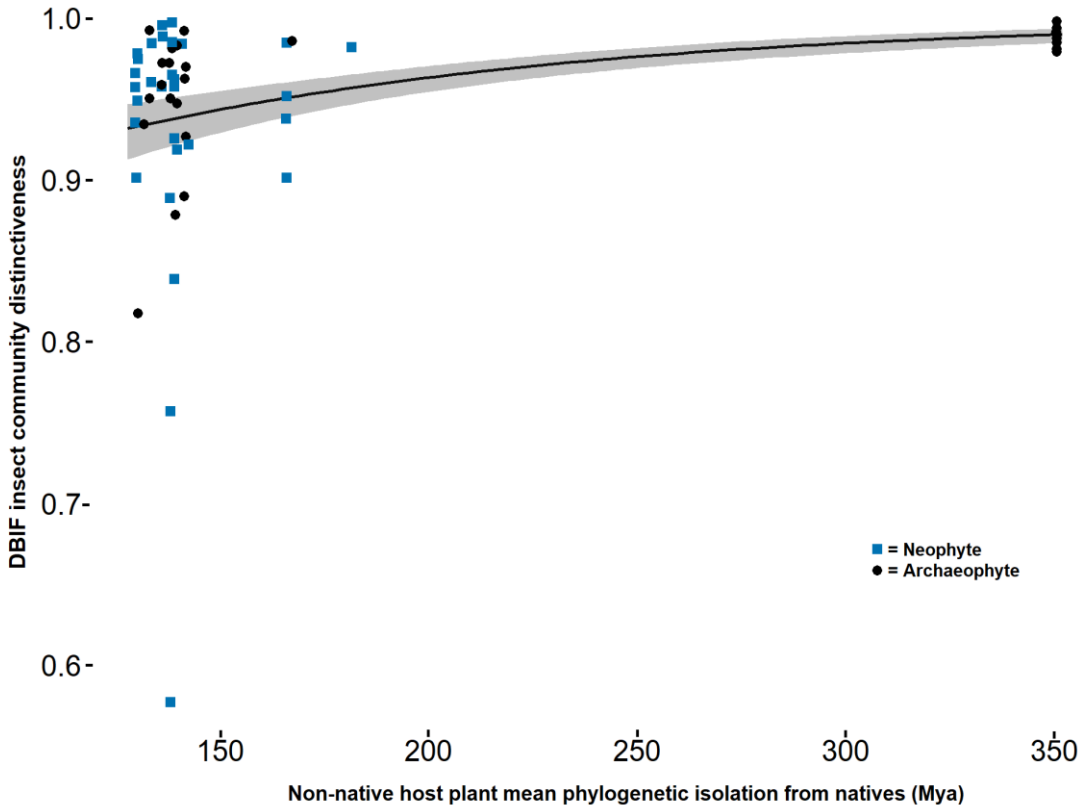

Figure A2.9: The effect of non-native host plant phylogenetic isolation on geographic-scale DBIF insect community distinctiveness. A partial regression plot displays the effect of our focal predictor (phylogenetic isolation), whilst holding all other predictors at their mean. Shaded areas represent 95% confidence intervals. Data points represent individual plants species. Non-native host plant mean phylogenetic isolation from natives (PIN) = mean distance in millions of years from *non-native* host plant to all other *native* plants in the DBIF. The distinctiveness of the insect community on a plant was represented by dissimilarity from the pool of insects found on native plants (see Methods). Beta model (DBIF Insect Community Distinctiveness ~ log(Sources) + PIN | PIN) n = 56, p(PIN) < 1e-04, pseudo R^2 = 0.277. See Methods for details of the calculation of pseudo R^2 and for the distinction between beta regression mean and precision submodels.

Table A2.2 Insect identification of local-scale Vortis samples for allocation of functional group

Taxonomic group	Level of Identification	Primary identification work
HEMIPTERA		
STERNORRHYNCHA	Suborder/Species	Hodkinson & White, 1979; Unwin, 2001
AUCHENORHYNCHA	Genus/Species	Le Quesne, 1965; Le Quesne & Payne, 1981
HETEROPTERA	Genus/Species	Southwood & Leston, 1959
COLEOPTERA		
Anthicidae	Species	Buck, 1954
Apionidae	Species	Morris, 1990
Carabidae	Species	Luff, 2007
Chrysomelidae	Genus/Species	Hubble, 2010
Coccinellidae	Species	Majerus & Kearns, 1989
Corylophidae	Family	Unwin, 1984
Curculionidae	Genus/Species	Joy, 1932; Duffy, 1953; Morris, 1990, 1997, 2008
Lathridiidae	Species	Hackston, 2018
Nanophydiae	Species	Morris, 1990
Nitidulidae	Species	Kirk-Spriggs, 1996
Oedemeridae	Species	Buck, 1954
Ptiliidae	Family	Unwin, 1984
Scraptiidae	Species	Levey, 2009
Staphylinidae	Family/Genus/Species	Joy, 1932
Tenebrionidae	Species	Buck, 1954
Throscidae	Species	Joy, 1932
OTHER ORDERS		
BLATTODEA	Species	Barnard, 2011
DERMAPTERA	Species	Hincks, 1949
ORTHOPTEROID	Species/Genus	Marshall & Haes, 1988

Table A2.3 Likelihood ratio tests – Vortis insect feeding type vs. plant native status or phylogenetic isolation

Response	Predictors without Interaction	Predictors with Interaction	χ2	*p*	*d.f.*
Abundance	Type + Status	Type*Status	8.641	0.195	6
Abundance	Type + Mean PI	Type*Mean PI	4.965	0.174	3
Abundance	Type + Mean PIN	Type*Mean PIN	5.444	0.142	3
Abundance	Type + NPN	Type*NPN	7.031	0.071	3
Abundance	Type + NPNN	Type*NPNN	6.190	0.103	3
Richness	Type + Status	Type*Status	8.157	0.227	6
Richness	Type + Mean PI	Type*Mean PI	2.092	0.554	3
Richness	Type + Mean PIN	Type*Mean PIN	2.832	0.418	3
Richness	Type + NPN	Type*NPN	5.561	0.135	3
Richness	Type + NPNN	Type*NPNN	2.638	0.451	3

Likelihood ratio tests determining the significance of the interaction between local-scale Vortis insect feeding type and plant native status, or phylogenetic isolation, when regressed against insect richness and abundance in separate negative binomial models. PI = phylogenetic isolation. PIN = phylogenetic isolation from natives. NPN = nearest phylogenetic neighbour distance. NPNN = nearest phylogenetic native neighbour distance. See Methods for details on the different phylogenetic isolation indices.

Table A2.4 Local-scale abundance models

Covariate/Contrast	*z*	*p*
VORTIS SAMPLING [ALL PLANTS]		
Model 1: **Vortis Insect Abundance ~ Status** [D^2 = 0.205, AIC = 409.4]		
Status (Overall)	NA	NA
Status Contrasts: C-N	-1.342	0.372
Status Contrasts: E-N	-3.520	0.001
Status Contrasts: E-C	-2.092	0.092
Model 2: **Vortis Insect Abundance ~ Status + Mean PI** [D^2 = 0.209, AIC= 411.2]		
Status (Overall)	NA	NA
Status Contrasts: C-N	-1.281	0.406
Status Contrasts: E-N	-3.514	0.001
Status Contrasts: E-C	-2.180	0.075
Mean PI	0.513	0.608
Model 3: **Vortis Insect Abundance ~ NPN** [D^2 = 0.108, AIC = 412.8]		
NPN	-2.800	0.005
VORTIS SAMPLING [NON-NATIVE PLANTS ONLY]		
Model 4: **Vortis Insect Abundance ~ Status + Mean PI from Natives** [D^2 = 0.111, AIC = 261.2]		
Status (E-C)	-1.794	0.073
Mean PI from Natives	-0.148	0.883
Model 5: **Vortis Insect Abundance ~ NPN from Natives** [D^2 = 0.103, AIC = 259.4]		
NPN from Natives	-1.93	0.054
POLLINATORS [ALL PLANTS]		
Model 6: **Pollinator Abundance ~ log(Replicates)** [D^2 = 0.485, AIC = 636.4]		
log(Replicates)	10.886	<1e-04
Model 7: **Pollinator Abundance ~ log(Replicates) + Flowering Units + Status** [D^2 = 0.624, 0.280 – 0.286, AIC = 620.43]		
log(Replicates)	10.859	<1e-04
Flowering Units	5.350	<1e-04
Status Overall	NA	NA
Status Contrasts: C-N	0.882	0.651
Status Contrasts: E-N	-1.324	0.382
Status Contrasts: E-C	-2.171	0.076
Model 8: **Pollinator Abundance ~ log(Replicates) + Flowering Units + Mean PI** [D^2 = 0.632, 0.209 – 0.381, AIC = 617.01]		
log(Replicates)	9.863	<1e-04
Flowering Units	4.803	<1e-04
Mean PI	-3.156	0.002

Model 9: **Pollinator Abundance ~ log(Replicates) + Flowering Units + NPN** [D^2 = 0.611, 0.215 – 0.363, AIC = 620.79]		
log(Replicates)	9.863	<1e-04
Flowering Units	5.275	<1e-04
NPN	-1.621	0.105
POLLINATORS [NON-NATIVE PLANTS ONLY]		
Model 10: **Pollinator Abundance ~ log(Replicates) + Flowering Units + Status + Mean PI from Natives** [D^2 = 0.641, 0.275 – 0.429, AIC = 391.87]		
log(Replicates)	7.120	<1e-04
Status (E-C)	1.918	0.055
Flowering Units	4.671	<1e-04
Mean PI from Natives	-1.668	0.095
Model 11: **Pollinator Abundance ~ log(Replicates) + Flowering Units + NPN from Natives** [D^2 = 0.595, 0.229 – 0.369, AIC = 395.22]		
log(Replicates)	7.552	<1e-04
Flowering Units	4.764	<1e-04
NPN from Natives	-0.898	0.369

Negative binomial models describing the effects of host plant native status, and/or host plant phylogenetic isolation, and several control variables (pollinator models only) on local-scale insect abundance. Contrasts calculated via post-hoc Tukey tests. N = native, C = congener, E = exotic, PI = phylogenetic isolation, NPN = nearest phylogenetic neighbour distance. D^2 represents the proportion of deviance explained by a model. D represents the range of deviance explained by all predictors of interest, after accounting for sampling effort (log(Replicates)) in pollinator models. Host plant native status did not significantly improve Model 8 (likelihood ratio test $\chi 2$ = 5.134, p = 0.077, d.f. = 2). See Methods for an explanation of the different phylogenetic isolation indices, of the calculation of D, and of the model building process.

Table A2.5 Local-scale richness models

Covariate/Contrast	*z*	*p*
VORTIS SAMPLING [ALL PLANTS]		
Model 1**: Vortis Insect Richness ~ Status** [D^2 = 0.163, AIC = 259.6]		
Status Overall	NA	NA
Status Contrasts: C-N	-1.915	0.134
Status Contrasts: E-N	-2.841	0.013
Status Contrasts: E-C	-0.843	0.676
Model 2: **Vortis Insect Richness ~ Status + Mean PI** [D^2 = 0.210, AIC = 259.0]		
Status Overall	NA	NA
Status Contrasts: C-N	-1.943	0.127
Status Contrasts: E-N	-3.172	0.004
Status Contrasts: E-C	-1.187	0.461
Mean PI	1.622	0.104
Model 3: **Vortis Insect Richness ~ NPN** [D^2 = 0.112, AIC = 260.1]		
NPN	-2.389	0.017
VORTIS SAMPLING [NON-NATIVE PLANTS ONLY]		
Model 4: **Vortis Insect Richness ~ Mean PI from Natives** [D^2 = 0.008, AIC = 169.9]		
Mean PI from Natives	0.497	0.619
Model 5: **Vortis Insect Richness ~ NPN from Natives** [D^2 = 0.036, AIC = 169.1]		
NPN from Natives	-1.075	0.282
POLLINATORS [ALL PLANTS]		
Model 6: **Pollinator Richness ~ log(Replicates)** [D^2 = 0.560, AIC = 350.6]		
log(Replicates)	8.825	<1e-04
Model 7: **Pollinator Richness ~ log(Replicates) + Flowering Units + Status** [D^2 = 0.636, D = 0.160 – 0.264, AIC = 342.6]		
log(Replicates)	8.938	<1e-04
Flowering Units	2.506	0.012
Status Overall	NA	NA
Status Contrasts: C-N	-0.534	0.854
Status Contrasts: E-N	-2.966	0.008
Status Contrasts: E-C	-2.411	0.042
Model 8: **Pollinator Richness ~ log(Replicates) + Flowering Units + Status + Mean PI** [D^2 = 0.671, D = 0.154 – 0.449, AIC = 337.4]		
log(Replicates)	8.236	<1e-04
Flowering Units	2.059	0.039
Status Overall	NA	NA
Status Contrasts: C-N	-0.746	0.736
Status Contrasts: E-N	-2.781	0.015
Status Contrasts: E-C	-2.030	0.105
Mean PI	-2.579	0.010

Model 9: **Pollinator Richness ~ log(Replicates) + Flowering Units + NPN** [D^2 = 0.611, D = 0.120 – 0.389, AIC = 340.7]		
log(Replicates)	8.228	<1e-04
Flowering Units	2.213	0.027
NPN	-3.016	0.003
POLLINATORS [NON-NATIVE PLANTS ONLY]		
Model 10: **Pollinator Richness ~ log(Replicates) + Flowering Units + Status + Mean PI from Natives** [D^2 = 0.665, D = 0.169 – 0.368, AIC = 207.8]		
log(Replicates)	7.025	<1e-04
Flowering Units	2.296	0.022
Status (E-C)	-2.326	0.020
Mean PI from Natives	-1.414	0.157
Model 11: **Pollinator Richness ~ log(Replicates) + Flowering Units + NPN from Natives** [D^2 = 0.628, D = 0.121 – 0.311, AIC = 210.8]		
log(Replicates)	6.823	<1e-04
Flowering Units	2.032	0.042
NPN from Natives	-2.065	0.039

Negative binomial models describing the effects of host plant native status, and/or host plant phylogenetic isolation, and several control variables (pollinator models only) on local-scale insect richness. Contrasts calculated via post-hoc Tukey tests. N = native, C = congener, E = exotic, PI = phylogenetic isolation, NPN = nearest phylogenetic neighbour distance. D^2 represents the proportion of deviance explained by a model. D represents the range of deviance explained by all predictors of interest, after accounting for sampling effort (log(Replicates)) in pollinator models. Host plant native status did not significantly improve Model 4 (likelihood ratio test $\chi 2 = 1.069$, $p = 0.301$, d.f. = 1). See Methods for an explanation of the different phylogenetic isolation indices, of the calculation of D, and of the model building process.

Table A2.6 Geographic-scale richness models

Covariate/Contrast	*z*	*p*
ALL PLANTS [NEGATIVE BINOMIAL MODELS]		
Model 1: **DBIF Insect Richness ~ log(Sources)** [D^2 = 0.920, AIC = 4512.1]		
log(Sources)	69.623	<1e-04
Model 2: **DBIF Insect Richness ~ log(Sources) + Hectads + Status** [D^2 = 0.924, D = 0.007 – 0.830, AIC = 4485.4]		
log(Sources)	58.739	<1e-04
No. of Hectads	4.881	<1e-04
Status Overall	NA	NA
N - ARCH	-0.263	0.962
NEO - ARCH	-1.373	0.350
NEO - N	-1.492	0.290
Model 3: **DBIF Insect Richness ~ log(Sources) + Hectads + Mean PI** [D^2 = 0.924, D = 0.009 – 0.828, AIC = 4484.3]		
log(Sources)	58.895	<1e-04
No. of Hectads	5.539	<1e-04
Mean PI	-1.254	0.210
Model 4: **DBIF Insect Richness ~ log(Sources) + Hectads + NPN** [D^2 = 0.924, D = 0.010 – 0.829, AIC = 4476.8]		
log(Sources)	59.115	<1e-04
No. of Hectads	5.386	<1e-04
NPN	-3.057	0.002
NON-NATIVE PLANTS ONLY [POISSON MODELS]		
Model 5: **DBIF Insect Richness ~ log(Sources)** [D^2 = 0.919, AIC = 1316.7]		
log(Sources)	53.794	<1e-04
Model 6: **DBIF Insect Richness ~ log(Sources) + Hectads + Status** [D^2 = 0.927, D = 0.025 – 0.763, AIC = 1293.5]		
log(Sources)	46.383	<1e-04
No. of Hectads	3.091	0.002
Status (NEO – ARCH)	-4.142	<1e-04
Model 7: **DBIF Insect Richness ~ log(Sources) + Hectads + Mean PI from Natives** [D^2 = 0.924, D = 0.014 – 0.769, AIC = 1301.4]		
log(Sources)	46.731	<1e-04
No. of Hectads	2.697	0.007
Mean PI from Natives	-2.989	0.003
Model 8: **DBIF Insect Richness ~ log(Sources) + Hectads + Mean PI from Natives + Status** [D^2 = 0.927, D = 0.016 – 0.795, AIC = 1293.6]		
log(Sources)	44.701	<1e-04
No. of Hectads	2.854	0.004
Mean PI from Natives	-1.360	0.174
Status (NEO – ARCH)	-3.109	0.002

Model 9: **DBIF Insect Richness ~ log(Sources) + Hectads + NPN from Natives** [D^2 = 0.924, D = 0.016 – 0.758, AIC = 1301.0]		
log(Sources)	46.961	<1e-04
No. of Hectads	2.899	0.004
NPN from Natives	-3.034	0.002
Model 10: **DBIF Insect Richness ~ log(Sources) + Hectads + NPN from Natives + Status** [D^2 = 0.927, D = 0.017 – 0.784, AIC = 1293.6]		
log(Sources)	45.109	< 2e-16
No. of Hectads	2.966	0.003
NPN from Natives	-1.370	0.171
Status (NEO – ARCH)	-3.063	0.002
NEOPHYTE PLANTS ONLY [POISSON MODELS]		
Model 11: **DBIF Insect Richness ~ log(Sources)** [D^2 = 0.914, AIC = 775.2]		
log(Sources)	37.830	<1e-04
Model 12: **DBIF Insect Richness ~ log(Sources) + Hectads + Time Since Neophyte Arrival** [D^2 = 0.923, D = 0.012 – 0.850, AIC = 767.7]		
log(Sources)	25.438	<1e-04
No. of Hectads	2.939	0.003
Neophyte Arrival Date	0.948	0.343

Poisson/negative binomial models describing the effects of host plant native status, neophyte host plant arrival date, host plant phylogenetic isolation, and host plant range size (no. of hectads) on geographic-scale DBIF insect richness. Contrasts calculated via post-hoc Tukey tests. N = native, C = congener, E = exotic, PI = phylogenetic isolation, NPN = nearest phylogenetic neighbour distance. D^2 represents the proportion of deviance explained by a model. D represents the range of deviance explained by all predictors of interest, after accounting for sampling effort (log(Sources)). Host plant native status did not significantly improve Models 3 and 4 (Model 3 likelihood ratio test $\chi 2 = 1.737$, $p = 0.420$, d.f. = 2; Model 4 likelihood ratio test $\chi 2 = 0.853$, $p = 0.653$, d.f. = 2). See Methods for an explanation of the different phylogenetic isolation indices, of the calculation of D, and of the model building process.

Table A2.7 Local-scale insect community distinctiveness models

Covariate/Contrast	*z*	*p*
VORTIS SAMPLING [ALL PLANTS]		
Model 1: **Vortis Insect Community Distinctiveness ~ Status** [Psuedo R^2 = 0.182, AIC = -63.3]		
Status Overall	NA	NA
Status Contrasts: C-N	2.586	0.026
Status Contrasts: E-N	2.833	0.013
Status Contrasts: E-C	0.162	0.986
Model 2: **Vortis Insect Community Distinctiveness ~ Status + Mean PI** [Psuedo R^2 = 0.187, AIC = -61.5]		
Status Overall	NA	NA
Status Contrasts: C-N	2.590	0.026
Status Contrasts: E-N	2.676	0.020
Status Contrasts: E-C	0.055	0.998
Mean PI	0.521	0.602
Model 3: **Vortis Insect Community Distinctiveness ~ NPN** [Psuedo R^2 = 0.005, AIC = -56.4]		
NPN	0.465	0.642
POLLINATORS [ALL PLANTS]		
Model 4: **Pollinator Community Distinctiveness ~ log(Replicates)** [Psuedo R^2 = 0.234, AIC = -91.0]		
log(Replicates)	-3.797	1.46e-04
Model 5: **Pollinator Community Distinctiveness ~ log(Replicates) + Flowering Units + Status | Status + Median Julian Sampling Date** [Psuedo R^2 = 0.235, AIC = -107.3]		
log(Replicates)	-4.459	<1e-04
Flowering Units	-2.483	0.013
Status Overall	NA	NA
Status Contrasts: C-N	3.905	2.85e-04
Status Contrasts: E-N	4.055	1.53e-04
Status Contrasts: E-C	1.333	0.372
Model 6: **Pollinator Community Distinctiveness ~ log(Replicates) + Flowering Units + Mean PI** [Psuedo R^2 = 0.291, AIC = -92.3]		
log(Replicates)	-4.132	<1e-04
Flowering Units	-1.826	0.068
Mean PI	0.973	0.331
Model 7: **Pollinator Community Distinctiveness ~ log(Replicates) + Flowering Units + NPN | Median Julian Sampling Date** [Psuedo R^2 = 0.291, AIC = -94.2]		
log(Replicates)	-3.914	<1e-04
Flowering Units	-1.799	0.072
NPN	1.309	0.191

Beta models describing the effects of host plant native status, and/or host plant phylogenetic isolation, and pollinator host plant replicate number, on local-scale insect community distinctiveness. Contrasts calculated via post-hoc Tukey tests. N = native, C = congener, E = exotic, PI = phylogenetic isolation, NPN = nearest phylogenetic neighbour distance. D^2 represents the proportion of deviance explained by a model. Beta regression mean submodel test values are reported above. See Methods for an explanation

of the different phylogenetic isolation indices and of the model building process, and for the distinction between beta regression mean and precision submodels.

The following $\chi 2$ statistics report the results of likelihood ratio tests used in the model building process. Host plant median volume did not significantly improve the mean submodel of Model 1 ($\chi 2 = 0.042$, $p = 0.837$, d.f. = 1) or the precision submodel ($\chi 2 = 1.672$, $p = 0.196$, d.f. = 1) and so was excluded from this and subsequent Vortis models. Host plant branching architecture did not significantly improve the mean submodel of Model 1 ($\chi 2 = 0.274$, $p = 0.601$, d.f. = 1) or the precision submodel ($\chi 2 = 2.241$, $p = 0.134$, d.f. = 1) and so was excluded from this and subsequent Vortis models. Host plant status did not significantly improve the precision submodel of Model 1 ($\chi 2 = 2.800$, $p = 0.247$, d.f. = 1), Model 2 ($\chi 2 = 2.731$, $p = 0.255$, d.f. = 1), or Model 6 ($\chi 2 = 3.448$, $p = 0.178$, d.f. = 1). Host plant status did not significantly improve the mean submodel of Model 6 ($\chi 2 = 0.644$, $p = 0.725$, d.f. = 1). Phylogenetic isolation did not significantly improve the precision submodel of Model 2 ($\chi 2 = 2.149$, $p = 0.143$, d.f. = 1) or Model 6 ($\chi 2 = 1.015$, $p = 0.314$, d.f. = 1). Nearest phylogenetic neighbour distance did not significantly improve the precision submodel of Model 3 ($\chi 2 = 0.148$, $p = 0.700$, d.f. = 1) or Model 7 ($\chi 2 = 1.833$, $p = 0.176$, d.f. = 1). Median Julian sampling date did not significantly improve the mean submodel of Model 5 ($\chi 2 = 0.086$, $p = 0.769$, d.f. = 1), Model 6 ($\chi 2 = 0.089$, $p = 0.766$, d.f. = 1), or Model 7 ($\chi 2 = 0.050$, $p = 0.823$, d.f. = 1). Median Julian sampling date did not significantly improve the precision submodel of Model 6 ($\chi 2 = 3.220$, $p = 0.073$, d.f. = 1). Host plant flowering units did not significantly improve the precision submodel of Model 5 ($\chi 2 = 0.143$, $p = 0.705$, d.f. = 1), Model 6 ($\chi 2 = 0.077$, $p = 0.782$, d.f. = 1), or Model 7 ($\chi 2 = 0.036$, $p = 0.851$, d.f. = 1). log(replicates) did not significantly improve the precision submodel of Model 4 ($\chi 2 = 0.874$, $p = 0.350$, d.f. = 1), Model 5 ($\chi 2 = 0.236$, $p = 0.627$, d.f. = 1), Model 6 ($\chi 2 = 0.115$, $p = 0.734$, d.f. = 1), or Model 7 ($\chi 2 = 0.787$, $p = 0.375$, d.f. = 1).

Table A2.8 Geographic-scale insect community distinctiveness models

Covariate/Contrast	*z*	*p*
NON-NATIVE PLANTS ONLY		
Model 1: **DBIF Community Distinctiveness ~ Sources** [Psuedo R^2 = 0.069, AIC = -201.4]		
Sources	-1.919	0.055
Model 2: **DBIF Community Distinctiveness ~ Sources + Status** [Psuedo R^2 = 0.104, AIC = -201.5]		
Sources	-2.135	0.033
Status (NEO – ARCH)	1.438	0.150
Model 3: **DBIF Community Distinctiveness ~ Sources + Mean PI from Natives | Mean PI from Natives** [Psuedo R^2 = 0.277, AIC = -220.0]		
Sources	-3.018	0.003
Mean PI from Natives	7.513	<1e-04
Model 4: **DBIF Community Distinctiveness ~ Sources + NPN from Natives | NPN from Natives** [Psuedo R^2 = 0.218, AIC = -211.1]		
Sources	-2.674	0.008
NPN from Natives	5.050	<1e-04
NEOPHYTE PLANTS ONLY		
Model 5: **DBIF Community Distinctiveness ~ Sources** [Psuedo R^2 = 0.013, AIC = -99.6]		
Sources	-0.450	0.653
Model 6: **DBIF Community Distinctiveness ~ Time Since Neophyte Arrival** [Psuedo R^2 = 0.010, AIC = -106.3]		
Time Since Neophyte Arrival	0.447	0.655

Beta models describing the effects of host plant phylogenetic isolation on geographic-scale DBIF insect community distinctiveness on non-natives plants. Contrasts calculated via post-hoc Tukey tests. NEO = neophyte, ARCH = archaeophyte, PI = phylogenetic isolation, NPN = nearest phylogenetic neighbour distance. Psuedo R^2 represents the proportion of variance explained by a model. Beta regression mean submodel test values are reported above. See Methods for an explanation of the different phylogenetic isolation indices and of the model building process, and for the distinction between beta regression mean and precision submodels.

The following $\chi 2$ statistics report the results of likelihood ratio tests used in the model building process. Host plant native status did not significantly improve the mean submodel of Model 1 ($\chi 2$ = 2.028, p = 0.154, d.f. = 1), Model 3 ($\chi 2$ = 0.006, p = 0.939, d.f. = 1), or Model 4 ($\chi 2$ = 0.034, p = 0.854, d.f. = 1). Host plant native status did not significantly improve the precision submodel of Model 1 ($\chi 2$ = 0.599, p = 0.439, d.f. = 1), Model 2 ($\chi 2$ = 0.022, p = 0.883, d.f. = 1), Model 3 ($\chi 2$ = 0.077, p = 0.781, d.f. = 1), or Model 4 ($\chi 2$ = 0.070, p = 0.791, d.f. = 1). Host plant range size did not significantly improve the mean submodel of Model 1 ($\chi 2$ = 1.121, p = 0.290, d.f. = 1) or the precision submodel ($\chi 2$ = 0.018, p = 0.892, d.f. = 1) and so was excluded from this and subsequent models. Sources did not significantly improve the mean submodel of Model 6 ($\chi 2$ = 1.177, p = 0.278, d.f. = 1), or the precision submodel of Model 1 ($\chi 2$ = 0.594, p = 0.441, d.f. = 1), Model 2 ($\chi 2$ = 0.022, p = 0.883, d.f. = 1), Model 3 ($\chi 2$ = 0.004, p = 0.949, d.f. = 1), Model 4 ($\chi 2$ = 0.029, p = 0.865, d.f. = 1), Model 5 ($\chi 2$ = 1.421, p = 0.233, d.f. = 1), or Model 6 ($\chi 2$ = 2.422, p = 0.120, d.f. = 1). Time since neophyte arrival did not significantly improve the precision submodel of Model 1 ($\chi 2$ = 0.917, p = 0.338, d.f. = 1) or Model 6 ($\chi 2$ = 1.238, p = 0.266, d.f. = 1).

Appendix 3 Supporting information for Chapter 4

Appendix 3A. R packages used for analysis

A list of R packages used for various functions is as follows: data manipulation = reshape (Wickham, 2007), plyr (Wickham, 2011), dplyr (Wickham, 2019), stringr (Wickham, 2017), and data.table (Dowle & Srinivasan, 2017); d' specialisation index calculation = bipartite (Dormann, Gruber, & Fruend, 2008); sample based rarefaction = iNEXT (Hsieh, Ma, & Chao, 2016); D^2 calculation = modEvA (Barbosa, Brown, Jimenez-Valverde, & Real, 2016); likelihood ratio tests = lmtest (Zeileis & Hothorn, 2002); Gamma GLMM models = lme4 (Bates, Maechler, Bolker, & Walker, 2015); beta GLM models = betreg (Cribari-Neto & Zeileis, 2010); post-hoc Tukey contrasts = multcomp (Hothorn, Bretz, & Westfall, 2008); figures = ggplot2 (Wickham, 2009); adding significance bars to box plots = ggsignif (Ahlmann-Eltze, 2017); beta regression figures = sjPlot (Lüdecke, 2019); Venn diagrams = limma (Ritchie et al., 2015).

Figure A3.1: The geographical distribution of RHS records across Great Britain. The 7,141 (~77%) records with British grid references are displayed here. 20 (<1%) records with Irish/Northern Irish grid references are not displayed here.

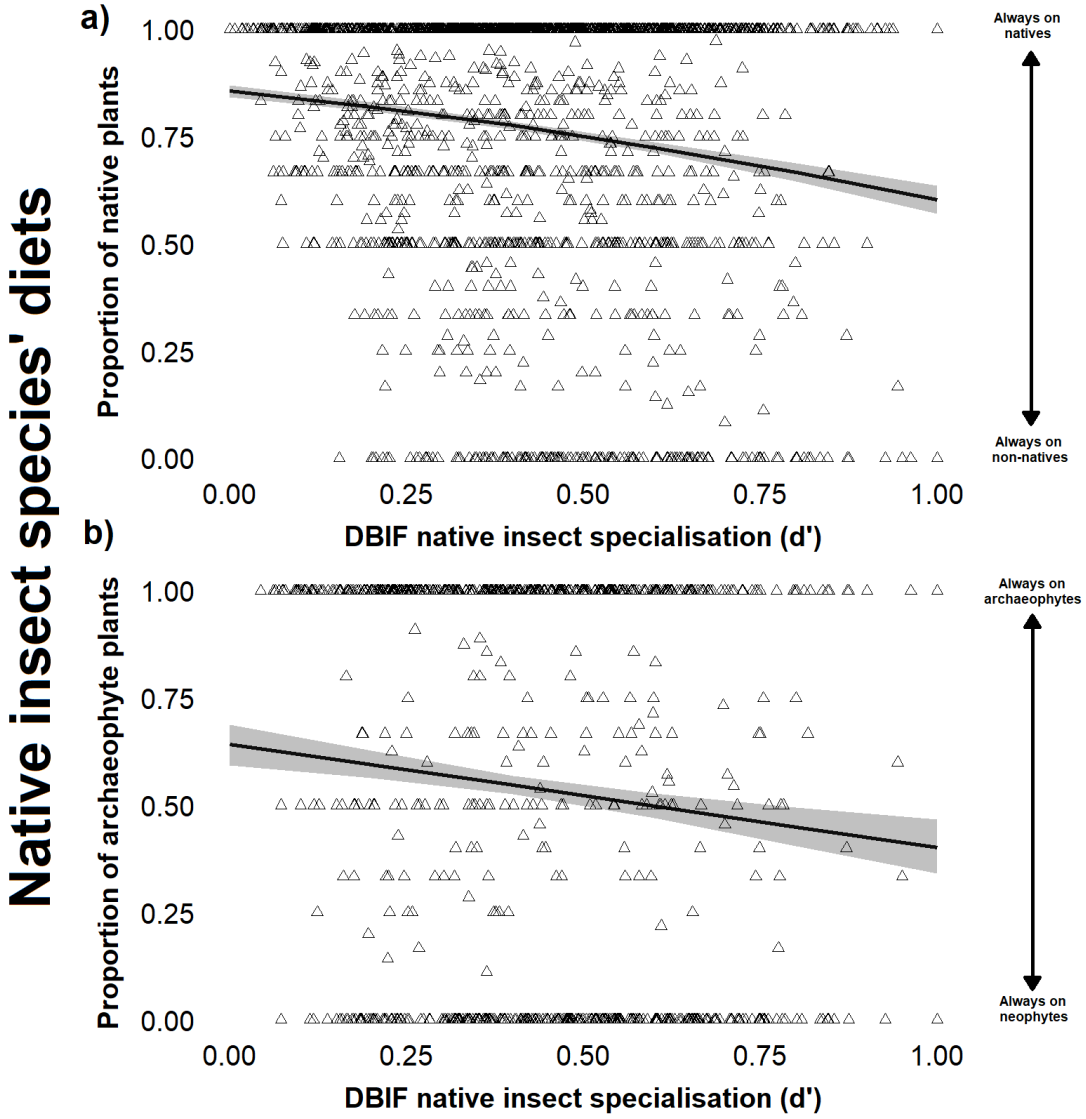

Figure A3.2: The effect of DBIF native insect specialism on host plant associations. DBIF insects were sampled in the wider countryside/outside of gardens. Beta regression tested the effect of insect species' specialism (d') on proportional use of different host plants. d' values ranged from 0 (perfect generalist) to 1 (perfect specialist). Pseudo R^2 represents the proportion of variance explained by a model. See Methods for details of host plant native status categories, the distinction between beta regression mean and precision submodels, and the calculation of d'.

a) beta GLM model (Records on Native Plants/Records on All Plants ~ d' | d') pseudo R^2 = 0.015, p(d') < 1e-04, number of DBIF native insect species = 4091.

b) beta GLM model (Records on Archaeophyte Plants/Records on All Non-Native Plants ~ d') psuedo R^2 = 0.031, p(d') < 1e04, number of DBIF native insect species = 994.

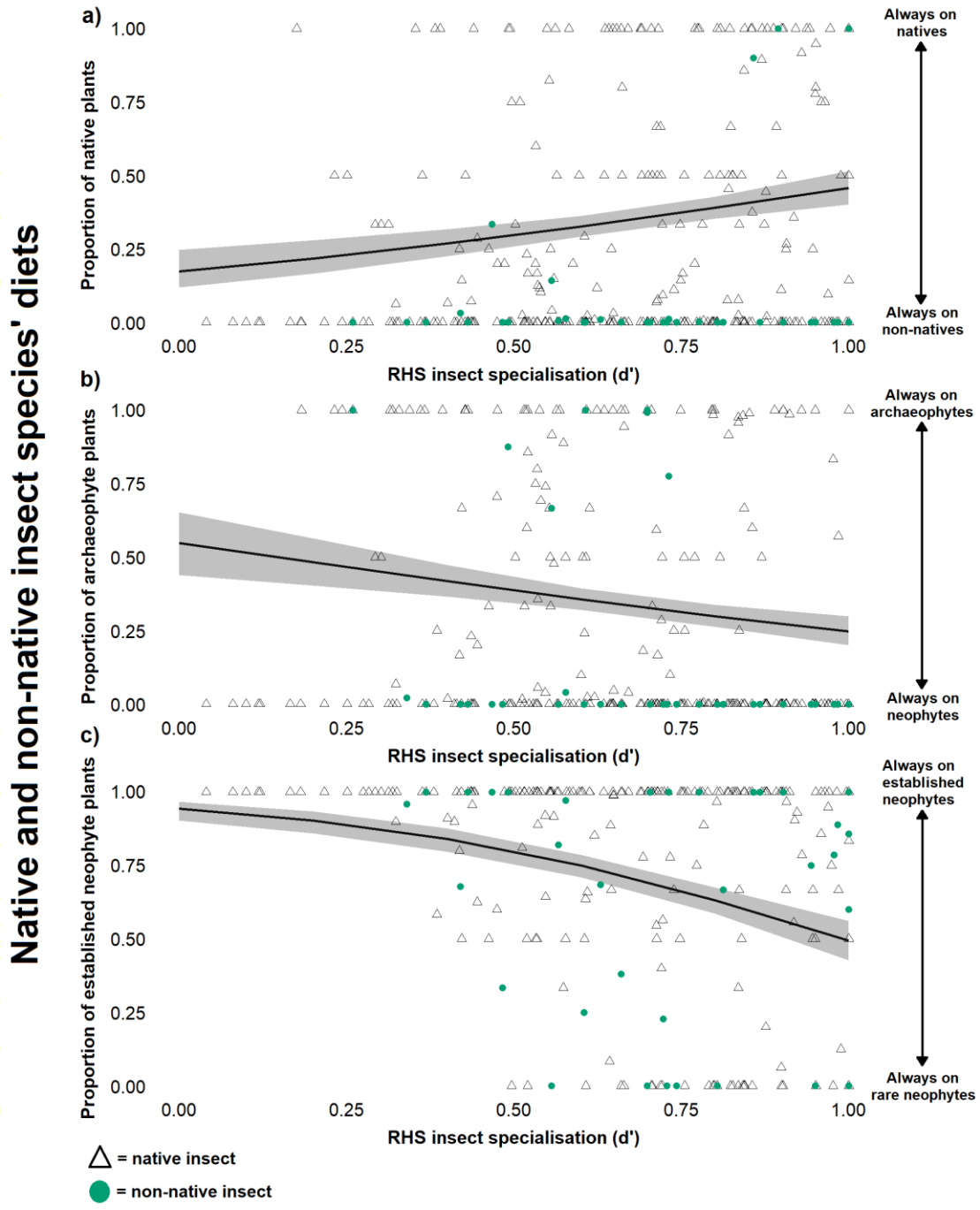

Figure A3.3: The effect of RHS insect specialism on host plant associations. RHS insects were sampled in novel garden ecosystems. Beta regression tested the effect of insect species' specialism (d') on proportional use of different host plants. d' values ranged from 0 (perfect generalist) to 1 (perfect specialist). Pseudo R^2 represents the proportion of variance explained by a model. See Methods for details of host plant native status categories, the distinction between beta regression mean and precision submodels, and the calculation of d'.

a) beta GLM model (Records on Native Plants/Records on All Plants ~ Insect Native Status + d' | Insect Native Status + d') pseudo R^2 = 0.067, p(d') < 1e-04, number of RHS native insect species = 364, RHS non-

native = 49. There was no significant interaction between insect native status and d' in the mean submodel (likelihood ratio test $\chi2 = 0.33$, $p = 0.565$, d.f. = 1).

b) beta GLM model (Records on Archaeophyte Plants/Records on All Non-Native Plants ~ d' | d') psuedo $R^2 = 0.055$, p(d') < 1e04, number of RHS native insect species = 297, RHS non-native = 46. Insect native status did not significantly improve the mean submodel (likelihood ratio test $\chi2 = 1.70$, $p = 0.193$, d.f. = 1).

c) beta GLM model (Records on Established Neophyte Plants/Records on All Neophyte Plants ~ Insect Native Status + d' | d') psuedo $R^2 = 0.145$, p(d') < 1e-04, number of RHS native insect species = 245, RHS non-native = 43. There was no significant interaction between insect native status and d' in the mean submodel (likelihood ratio test $\chi2 = 0.27$, $p = 0.601$, d.f. = 1).

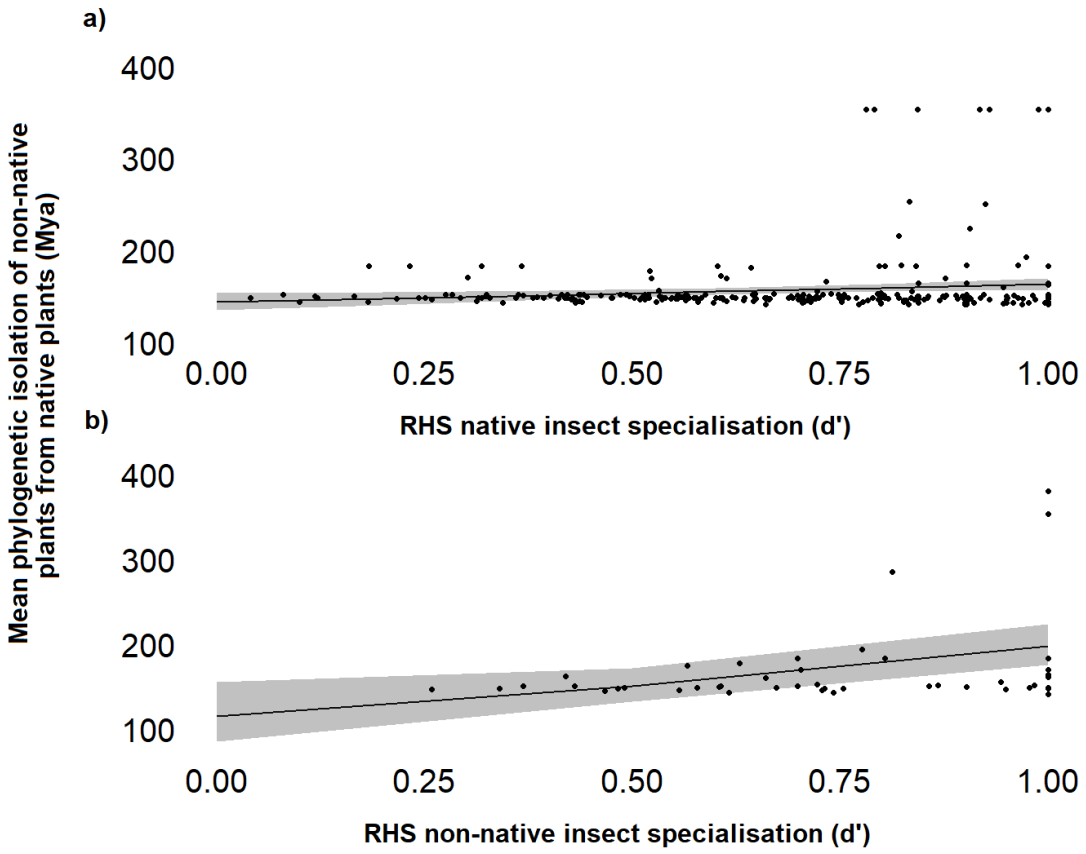

Figure A3.4: The association of RHS native and non-insect specialism with non-native host plant phylogenetic isolation. RHS insects were sampled in novel garden ecosystems. GLMs analysed the mean phylogenetic isolation of the non-native host plants associated with each insect species. D^2 represents the proportion of deviance explained by insect specialism. d' = insect specialism. See Methods for details of the calculation of phylogenetic isolation, and the calculation of d'.

a) Gamma GLM model (Non-Native Plant Mean Phylogenetic Isolation from Natives ~ RHS Native Insect Specialism) $D^2 = 0.035$, p(d') = 0.008. Number of RHS native insect species = 314.

b) Gamma GLM model (Non-Native Plant Mean Phylogenetic Isolation from Natives ~ RHS Non-Native Insect Specialism) $D^2 = 0.181$, p(d') = 0.007. Number of RHS non-native insect species = 49.

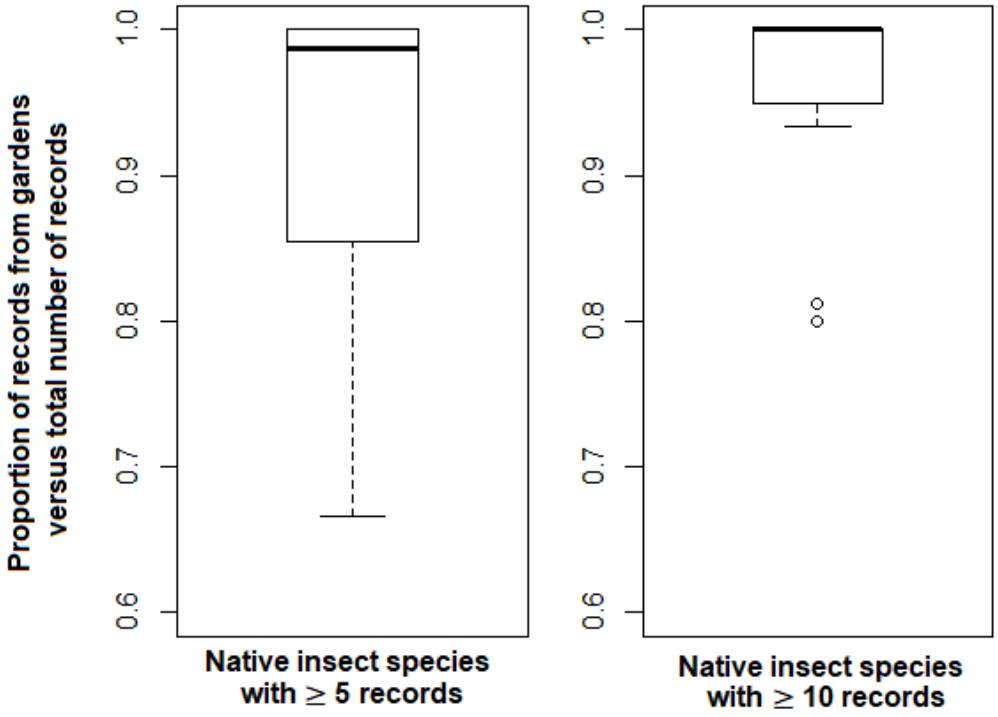

Figure A3.5: The proportion of records from gardens (RHS) versus the total number of records of each native insect species that was exclusively sampled on non-native plants across both datasets, and with the number of records across the two datasets ≥ 5 and ≥ 10. Number of insect species with number of records ≥ 5 = 46, number of records ≥ 10 = 24. Proportions were calculated for each native insect species as: the number of RHS records ÷ the total number of records within the RHS and DBIF datasets.

Table A3.1: The geographic origin of all RHS non-native insects

Non-Native Insect Species	Geographical Origin	Source
Adelges cooleyi	New World	GBNNSIP
Andricus quercuscalicis	Europe/North Africa	GBNNSIP
Aphalara itadori	Asia	GBNNSIP
Aphis gossypii	Europe/North Africa	GBNNSIP
Arge berberidis	Europe/North Africa	GBNNSIP
Aspidiotus nerii	Europe/North Africa	GBNNSIP
Bruchus pisorum	Europe/North Africa	GBNNSIP
Cameraria ohridella	Europe/North Africa	GBNNSIP
Cerataphis lataniae	Asia	Howard, Moore, Giblin-Davis, & Abad, 2001
Chrysolina americana	Europe/North Africa	GBNNSIP
Coccus hesperidum	Asia	Lagowska et al., 2015
Crioceris asparagi	Europe/North Africa	GBNNSIP
Dasineura gleditchiae	New World	GBNNSIP
Dryocosmus kuriphilus	Asia	GBNNSIP
Epiphyas postvittana	Australasia	GBNNSIP
Eriosoma lanigerum	Europe/North Africa	GBNNSIP
Eulecanium excrescens	Asia	GBNNSIP
Frankliniella occidentalis	New World	GBNNSIP
Heliothrips haemorrhoidalis	New World	GBNNSIP
Homotoma ficus	Europe/North Africa	GBNNSIP
Icerya purchasi	Australasia	GBNNSIP
Idiopterus nephrelepidis	New World	GBNNSIP
Leptinotarsa decemlineata	New World	GBNNSIP
Macrosiphum albifrons	New World	GBNNSIP
Myzus persicae	Europe/North Africa	GBNNSIP
Nezara viridula	Europe/North Africa	GBNNSIP
Panonychus citri	Asia	Kennett, McMurtry, & Beardsley, 1999
Paralipsa gularis	Asia	GBNNSIP
Parthenothrips dracaenae	Australasia	GBNNSIP
Phyllonorycter leucographella	Europe/North Africa	GBNNSIP
Phytomyza gymnostoma	Europe/North Africa	GBNNSIP
Pineus strobi	New World	GBNNSIP
Planococcus vovae	Europe/North Africa	GBNNSIP
Pseudococcus calceolariae	Australasia	GBNNSIP
Pulvinaria hydrangeae	Asia	GBNNSIP
Pulvinaria regalis	Asia	GBNNSIP
Saissetia oleae	Afrotropical	CABI, 2019
Sitophilus oryzae	Asia	Roques et al., 2010
Stegobium paniceum	Cosmopolitan	Bousquet, 1990

Stephanitis takeyai	Asia	GBNNSIP
Stigmella suberivora	Europe/North Africa	GBNNSIP
Takecallis arundicolens	Asia	GBNNSIP
Thrips simplex	Australasia	GBNNSIP
Trioza alacris	Europe/North Africa	GBNNSIP
Trioza vitreoradiata	Australasia	GBNNSIP
Vasates quadripedes	New World	GBNNSIP
Wahlgreniella nervata	New World	GBNNSIP

Insect geographic origins were obtained from the Great Britain Non-native Species Information Portal (GBNNSIP; NNSS 2019), and via an additional literature search for six uncertain cases. There were five insect species that occurred in Europe/North Africa and in one or more other categories (but were not cosmopolitan). These insects were classified as Europe/North Africa.

Table A3.2: The effect of insect native status and ecosystem type on host plant interaction frequencies (χ^2)

RHS Native vs. RHS Non-Native Insect - Plant Status Comparisons	χ^2	d.f	p
Overall (Native vs. Archaeophyte vs. Established Neophyte vs. Garden Neophyte)	517.18	3	< 1e-04
Native vs. Non-Native	331.00	1	< 1e-04
Native vs. Archaeophyte	121.24	1	< 1e-04
Native vs. Established Neophyte	330.86	1	< 1e-04
Native vs. Garden Neophyte	466.99	1	< 1e-04
Archaeophyte vs. Established Neophyte	84.83	1	< 1e-04
Archaeophyte vs. Garden Neophyte	179.34	1	< 1e-04
Established Neophyte vs. Garden Neophyte	61.62	1	< 1e-04
RHS Native vs. DBIF Native Insect - Plant Status Comparisons	**χ^2**	**d.f**	**p**
Overall (Native vs. Archaeophyte vs. Neophyte)	8173.09	2	< 1e-04
Native vs. Non-Native	8819.14	1	< 1e-04
Native vs. Archaeophyte	2156.09	1	< 1e-04
Native vs. Neophyte	8835.58	1	< 1e-04
Archaeophyte vs. Neophyte	1014.95	1	< 1e-04

χ^2 tests of the proportional use of host plants by insects. RHS insects were sampled in novel garden ecosystems, and DBIF insects were sampled in the wider landscape. RHS established and garden neophyte plants were treated together as neophytes for comparison of RHS native and DBIF native insects. See Methods for details of host plant native status categories.

Table A3.3: The effect of insect native status, ecosystem type, and specialism on host plant use (beta GLM)

Covariate/Contrast	z	p
Model 1 **Insect Species:** DBIF Native + RHS Native + RHS Non-Native **Model Specification:** *Records on Native Plants/Records on All Plants* *~ Insect Native Status/Ecosystem Type | Insect Native Status/Ecosystem Type* **Psuedo R^2** = 0.224 **Number of Insect Species:** DBIF Native = 4091, RHS Native = 364, RHS Non-Native = 51		
Contrast: DBIF Native vs. RHS Native	21.53	< 1e-04
Contrast: DBIF Native vs. RHS Non-Native	10.60	< 1e-04
Contrast: RHS Native vs. RHS Non-Native	3.22	0.003
Model 2 **Insect Species:** DBIF Native + RHS Native + RHS Non-Native **Model Specification:** *Records on Archaeophyte Plants/Records on All Non-Native Plants* *~ Insect Native Status/Ecosystem Type | Insect Native Status/Ecosystem Type* **Psuedo R^2** = 0.088 **Number of Insect Species:** DBIF Native = 994, RHS Native = 297, RHS Non-Native = 48		
Contrast: DBIF Native vs. RHS Native	7.87	< 0.001
Contrast: DBIF Native vs. RHS Non-Native	5.67	< 0.001
Contrast: RHS Native vs. RHS Non-Native	2.41	0.037
Model 3 **Insect Species:** DBIF Native **Model Specification:** *Records on Native Plants/Records on All Plants ~ d' | d'* **Psuedo R^2** = 0.015 **Number of Insect Species** = 4091		
Insect Specialism (d')	-11.88	< 1e-04
Model 4 **Insect Species:** DBIF Native **Model Specification:** *Records on Archaeophyte Plants/Records on All Plants ~ d'* **Psuedo R^2** = 0.031 **Number of Insect Species =** 994		
Insect Specialism (d')	-4.36	< 1e-04
Model 5 **Insect Species:** RHS Native + RHS Non-Native **Model Specification:** *Records on Native Plants/Records on All Plants ~ Insect Native Status + d' | Insect Native Status + d'* **Psuedo R^2** = 0.067 **Number of Insect Species**: RHS Native = 364, RHS Non-Native = 49		
Insect Native Status (RHS Native – RHS Non-Native)	3.91	< 1e-04
Insect Specialism (d')	4.55	< 1e-04
Model 6 **Insect Species:** RHS Native + RHS Non-Native **Model Specification:** *Records on Archaeophyte Plants/Records on All Non-Native Plants ~ d' | d'* **Psuedo R^2** = 0.055 **Number of Insect Species**: RHS Native = 297, RHS Non-Native = 46		
Insect Specialism (d')	-4.12	< 1e-04

Model 7 **Insect Species:** RHS Native + RHS Non-Native **Model Specification:** *Records on Established Neophyte Plants/Records on All Neophyte Plants ~ Insect Native Status + d' | d'* **Psuedo R^2** = 0.145 **Number of Insect Species**: RHS Native = 245, RHS Non-Native = 43		
Insect Native Status (RHS Native - RHS Non-Native)	1.82	0.068
Insect Specialism (d')	-7.58	< 1e-04

Beta regression tested the effect of insect species' native status, ecosystem type, and/or specialism on proportional use of different host plants. RHS insects were sampled in novel garden ecosystems, and DBIF insects were sampled in the wider landscape. Beta regression mean submodel test values are reported above. Contrasts calculated via post-hoc Tukey tests. Psuedo R^2 represents the proportion of variance explained by a model. RHS established and garden neophyte plants were treated together as neophytes for comparison of RHS native and DBIF native insects. Contrasts of DBIF native and RHS non-native insects are reported above, but are not included in Fig. 4.2, and are not interpreted in the Discussion. See Methods for details of host plant native status categories, the distinction between beta regression mean and precision submodels, and calculation of the d' index.

The following $\chi 2$ statistics report the results of likelihood ratio tests used in the model building process. There was no significant interaction between insect native status and d' in the mean submodels in Models 5 ($\chi 2 = 0.33$, $p = 0.565$, d.f. = 1) and 7 ($\chi 2 = 0.27$, $p = 0.601$, d.f. = 1). Insect native status did not significantly improve the mean submodel in Model 6 ($\chi 2 = 1.70$, $p = 0.193$, d.f. = 1), or the precision submodel in Model 6 ($\chi 2 = 0.17$, $p = 0.680$, d.f. = 1) and Model 7 ($\chi 2 = 1e\text{-}05$, $p = 0.998$, d.f. = 1). d' did not significantly improve the precision submodel in Model 4 ($\chi 2 = 0.45$, $p = 0.503$, d.f. = 1).

Table A3.4: The effect of ecosystem type on native insect host plant use (beta GLM)

Covariate/Contrast	z	p
Model 1 **Insect Species:** DBIF Native + RHS Native **Model Specification:** *Records on Native Plants/Records on All Plants ~ Ecosystem Type | Ecosystem Type* **Psuedo R^2** = 0.162 **Number of Insect Species:** DBIF Native = 253, RHS Native = 253		
Ecosystem Type (DBIF Native – RHS Native)	8.04	< 1e-04
Model 2 **Insect Species:** DBIF Native + RHS Native **Model Specification:** *Records on Archaeophyte Plants/Records on All Non-Native Plants ~ Ecosystem Type* **Psuedo R^2** = 0.033 **Number of Insect Species:** DBIF Native = 153, RHS Native = 153		
Ecosystem Type (DBIF Native – RHS Native)	2.60	0.009

Beta regression tested the effect of ecosystem type (RHS = novel garden ecosystems, DBIF = the wider landscape) on proportional use of different host plants by native insect species that were sampled within both datasets. Beta regression mean submodel test values are reported above. Psuedo R^2 represents the proportion of variance explained by a model. See Methods for details of host plant native status categories and the distinction between beta regression mean and precision submodels.

Ecosystem type did not significantly improve the precision submodel in Model 2 (likelihood ratio test $\chi 2$ = 0.14, p = 0.708, d.f. = 1).

Table A3.5: The association of insect native status, ecosystem type, or specialism with non-native plant phylogenetic isolation (Gamma GLMM)

Covariate	t	p
Model 1 **Insect Individuals:** RHS Native + RHS Non-Native **Model Specification:** *Non-Native Plant **Mean PI** from Natives ~ Insect Native Status + (1|Insect Genus)* **Marginal Psuedo R^2** = 0.055 **Conditional Pseudo R^2** = 0.684 **Number of Insect Records:** RHS Native = 5563, RHS Non-Native = 2073 **Number of Insect Genera =** 78		
Insect Native Status (RHS Native – RHS Non-Native)	-11.03	< 1e-04
Model 2 **Insect Individuals:** RHS Native + RHS Non-Native **Model Specification:** *Non-Native Plant **NPN** from Natives ~ Insect Native Status + (1|Insect Genus)* **Marginal Psuedo R^2** = 0.028 **Conditional Pseudo R^2** = 0.448 **Number of Insect Records:** RHS Native = 5563, RHS Non-Native = 2073 **Number of Insect Genera =** 78		
Insect Native Status (RHS Native – RHS Non-Native)	-7.71	< 1e-04
Model 3 **Insect Individuals:** DBIF Native + RHS Native **Model Specification:** *Non-Native Plant **Mean PI** from Natives ~ Ecosystem Type + (1|Insect Genus)* **Marginal Psuedo R^2** = 2.83e-06 **Conditional Pseudo R^2** = 0.830 **Number of Insect Records:** DBIF Native = 1084, RHS Native = 5666 **Number of Insect Genera =** 111		
Ecosystem Type (DBIF Native – RHS Native)	0.21	0.836
Model 4 **Insect Individuals:** DBIF Native + RHS Native **Model Specification:** *Non-Native Plant **NPN** from Natives ~ Ecosystem Type + (1|Insect Genus)* **Marginal Psuedo R^2** = 3.26e-05 **Conditional Pseudo R^2** = 0.265 **Number of Insect Records:** DBIF Native = 1084, RHS Native = 5666 **Number of Insect Genera =** 111		
Ecosystem Type (DBIF Native – RHS Native)	0.48	0.632
Model 5 **Insect Individuals:** DBIF Native **Model Specification:** *Non-Native Plant **Mean PI** from Natives ~ d' + (1|Insect Genus)* **Marginal Psuedo R^2** = 0.008 **Conditional Pseudo R^2** = 0.742 **Number of Insect Records:** DBIF Native = 882 **Number of Insect Genera =** 50		
Insect Specialism (d')	3.39	< 0.001
Model 6 **Insect Individuals:** DBIF Native **Model Specification:** *Non-Native Plant **NPN** from Natives ~ d' + (1|Insect Genus)* **Marginal Psuedo R^2** = 0.012 **Conditional Pseudo R^2** = 0.292 **Number of Insect Records:** DBIF Native = 882 **Number of Insect Genera =** 50		
Insect Specialism (d')	3.70	< 0.001

GLMMs analysed the phylogenetic isolation of all host plants for a subset of insect genera that interacted with non-native plants 10 or more times, following standard practice for GLMM random effect sample sizes (Bolker *et al.* 2009). RHS insects were sampled in novel garden ecosystems, and DBIF insects were sampled in the wider landscape. PI = phylogenetic isolation. NPN = nearest phylogenetic neighbour distance. Contrasts calculated via post-hoc Tukey tests. Marginal psuedo R^2 represents the proportion of variance uniquely explained by model fixed effects, and conditional pseudo R^2 represents the proportion of variance explained by both fixed and random (insect genus) effects. See Methods for details of host plant native status categories and calculation of the d' index.

Insect specialism (d') was a non-significant predictor of mean PI in Model 1 ($t = 0.51$, $p = 0.608$, d.f. = 7556), and NPN in model 2 ($t = -1.05$ $p = 0.291$, d.f. = 7556), and so was not included in the final models.

Table A3.6: The association of insect native status, ecosystem type, or specialism with mean non-native plant phylogenetic isolation (Gamma GLM)

Covariate	z	p
Model 1 **Insect Species:** RHS Native + RHS Non-Native **Model Specification:** *Non-Native Plant **Mean PI** from Natives ~ Insect Native Status + d'* **D^2** = 0.091 **Number of Insect Species**: RHS Native = 314, RHS Non-Native = 49		
Insect Native Status (RHS Native – RHS Non-Native)	-2.72	0.007
Insect Specialism (d')	3.57	< 0.001
Model 2 **Insect Species:** RHS Native + RHS Non-Native **Model Specification:** *Non-Native Plant **Mean PI** from Natives ~ Insect Native Status*d'* **D^2** = 0.120 **Number of Insect Species**: RHS Native = 314, RHS Non-Native = 49		
Insect Native Status (RHS Native – RHS Non-Native)	1.91	0.057
Insect Specialism (d')	2.51	0.013
Insect Native Status (RHS Native – RHS Non-Native) * Insect Specialism (d')	-2.77	0.006
Model 3 **Insect Species:** RHS Native **Model Specification:** *Non-Native Plant **Mean PI** from Natives ~ d'* **D^2** = 0.035 **Number of Insect Species**: RHS Native = 314		
Insect Specialism (d')	2.69	0.008
Model 4 **Insect Species:** RHS Non-Native **Model Specification:** *Non-Native Plant **Mean PI** from Natives ~ d'* **D^2** = 0.181 **Number of Insect Species**: RHS Non-Native = 49		
Insect Specialism (d')	2.82	0.007
Model 5 **Insect Species:** RHS Native + RHS Non-Native **Model Specification:** *Non-Native Plant **NPN** from Natives ~ Insect Native Status + d'* **D^2** = 0.095 **Number of Insect Species**: RHS Native = 314, RHS Non-Native = 49		
Insect Native Status (RHS Native – RHS Non-Native)	-4.61	< 1e-04
Insect Specialism (d')	1.85	0.065
Model 6 **Insect Species:** DBIF Native + RHS Native **Model Specification:** *Non-Native Plant **Mean PI** from Natives ~ Ecosystem Type* **D^2** = 0.005 **Number of Insect Species**: DBIF Native = 994, RHS Native = 314		
Ecosystem Type (DBIF Native – RHS Native)	2.06	0.039
Model 7 **Insect Species:** DBIF Native + RHS Native **Model Specification:** *Non-Native Plant **NPN** from Natives ~ Ecosystem Type* **D^2** = 0.002 **Number of Insect Species**: DBIF Native = 994, RHS Native = 314		
Ecosystem Type (DBIF Native – RHS Native)	1.36	0.180

Model 8 **Insect Species:** DBIF Native **Model Specification:** *Non-Native Plant **Mean PI** from Natives ~ d'* **D^2** = 0.004 **Number of Insect Species**: DBIF Native = 994		
Insect Specialism (d')	1.57	0.117
Model 9 **Insect Species:** DBIF Native **Model Specification:** *Non-Native Plant **NPN** from Natives ~ d' + Sampling Effort* **D^2** = 0.008 **Number of Insect Species**: DBIF Native = 994		
Insect Specialism (d')	1.14	0.255
Sampling Effort	-1.51	0.131

GLMs analysed the mean phylogenetic isolation of the host plants associated with each insect species. RHS insects were sampled in novel garden ecosystems, and DBIF insects were sampled in the wider landscape. PI = phylogenetic isolation. NPN = nearest phylogenetic neighbour distance. Contrasts calculated via post-hoc Tukey tests. D^2 represents the proportion of deviance explained by a model. See Methods for details host plant native status categories, estimation of sampling effort, and calculation of the d' index.

The following $\chi 2$ statistics report the results of likelihood ratio tests used in the model building process. There was no significant interaction between insect native status and d' in Model 5 ($\chi 2 = 1.01$, $p = 0.316$, d.f. = 1). Sampling effort did not significantly improve Model 1 ($\chi 2 = 0.32$, $p = 0.575$, d.f. = 1), Model 2 ($\chi 2 = 0.09$, $p = 0.761$, d.f. = 1), Model 3 ($\chi 2 = 0.88$, $p = 0.349$, d.f. = 1), Model 4 ($\chi 2 = 0.33$, $p = 0.565$, d.f. = 1), Model 5 ($\chi 2 = 3.12$, $p = 0.077$, d.f. = 1), Model 6 ($\chi 2 = 0.38$, $p = 0.540$, d.f. = 1), Model 7 ($\chi 2 = 0.002$, $p = 0.966$, d.f. = 1), or Model 8 ($\chi 2 = 3.35$, $p = 0.067$, d.f. = 1).

Table A3.7: The effect of RHS non-native insect geographical origin on host plant phylogenetic isolation (Gamma GLMM)

Contrast	z	p
Model 1 **Model Specification:** *Non-Native Plant **Mean PI** from Natives ~ Insect Origin + (1|Insect Genus)* **Marginal Psuedo R^2** = 0.101, **Conditional Pseudo R^2** = 0.514 **Number of Insect Records:** Afrotropical = 12, Asia = 862, Australasia = 32, Europe/North Africa = 1064, New World = 87 **Number of Insect Genera =** 15		
Asia - Afrotropical	1.73	0.385
Australasia - Afrotropical	-0.96	0.855
Europe/North Africa - Afrotropical	1.45	0.561
New World - Afrotropical	0.58	0.974
Australasia - Asia	-4.28	< 0.001
Europe/North Africa - Asia	-0.67	0.956
New World - Asia	-1.65	0.433
Europe/North Africa - Australasia	8.61	< 1e-04
New World - Australasia	2.42	0.096
New World - Europe/North Africa	-1.32	0.653
Model 2 **Model Specification:** *Non-Native Plant **NPN** from Natives ~ Insect Origin + (1|Insect Genus)* **Marginal Psuedo R^2** = 0.046, **Conditional Pseudo R^2** = 0.924 **Number of Insect Records:** Afrotropical = 12, Asia = 862, Australasia = 32, Europe/North Africa = 1064, New World = 87 **Number of Insect Genera =** 15		
Asia - Afrotropical	0.41	0.992
Australasia - Afrotropical	-0.49	0.985
Europe/North Africa - Afrotropical	0.06	1.000
New World - Afrotropical	-0.06	1.000
Australasia - Asia	-1.46	0.535
Europe/North Africa - Asia	-0.60	0.969
New World - Asia	-0.67	0.955
Europe/North Africa - Australasia	6.93	< 1e-04
New World - Australasia	0.66	0.956
New World - Europe/North Africa	-0.20	1.000

GLMMs analysed the phylogenetic isolation of all host plants for a subset of insect genera that interacted with non-native plants 10 or more times, following standard practice for GLMM random effect sample sizes (Bolker *et al.* 2009). RHS insects were sampled in novel garden ecosystems. PI = phylogenetic isolation. NPN = nearest phylogenetic neighbour distance. Contrasts calculated via post-hoc Tukey tests. Marginal psuedo R^2 represents the proportion of variance uniquely explained by model fixed effects, and conditional pseudo R^2 represents the proportion of variance explained by both fixed and random (insect genus) effects.

Table A3.8: The effect of RHS non-native insect geographical origin on mean host plant phylogenetic isolation per insect (Gamma GLM)

Contrast	z	p
Model 1 **Model Specification:** *Non-Native Plant **Mean PI** from Natives ~ Insect Origin* **D^2** = 0.155 **Number of Insect Species:** Afrotropical = 1, Asia = 12, Australasia = 6, Europe/North Africa = 17, New World = 10, Cosmopolitan = 1		
Asia - Afrotropical	0.54	0.993
Australasia - Afrotropical	0.29	1.000
Cosmopolitan - Afrotropical	0.03	1.000
Europe/North Africa - Afrotropical	0.49	0.996
New World - Afrotropical	1.21	0.812
Australasia - Asia	-0.50	0.995
Cosmopolitan - Asia	-0.50	0.995
Europe/North Africa - Asia	-0.16	1.000
New World - Asia	1.64	0.536
Cosmopolitan - Australasia	-0.25	1.000
Europe/North Africa - Australasia	0.40	0.998
New World - Australasia	1.84	0.402
Europe/North Africa - Cosmopolitan	0.45	0.997
New World - Cosmopolitan	1.16	0.834
New World - Europe/North Africa	1.91	0.360
Model 2 **Model Specification:** *Non-Native Plant **NPN** from Natives ~ Insect Origin + Sampling Effort* **D^2** = 0.189 **Number of Insect Species:** Afrotropical = 1, Asia = 12, Australasia = 6, Europe/North Africa = 17, New World = 10, Cosmopolitan = 1		
Asia - Afrotropical	0.17	1.000
Australasia - Afrotropical	0.49	0.996
Cosmopolitan - Afrotropical	-1.23	0.797
Europe/North Africa - Afrotropical	-0.01	1.000
New World - Afrotropical	0.71	0.978
Australasia - Asia	0.70	0.979
Cosmopolitan - Asia	-1.84	0.401
Europe/North Africa - Asia	-0.49	0.996
New World - Asia	1.30	0.760
Cosmopolitan - Australasia	-2.11	0.252
Europe/North Africa - Australasia	-1.12	0.856
New World - Australasia	0.41	0.998
Europe/North Africa - Cosmopolitan	1.69	0.504
New World - Cosmopolitan	2.37	0.144
New World - Europe/North Africa	1.86	0.393
Sampling Effort	2.38	0.022

GLMs analysed the mean phylogenetic isolation of the host plants associated with each insect species. RHS insects were sampled in novel garden ecosystems. PI = phylogenetic isolation. NPN = nearest phylogenetic neighbour distance. Contrasts calculated via post-hoc Tukey tests. D^2 represents the proportion of deviance explained by a model. Sampling effort did not significantly improve Model 1 ($\chi 2$ = 0.13, p = 0.714, d.f. = 1). See Methods for details of the estimation of sampling effort.

Table A3.9: Native insects uniquely associated with non-native plants across both the RHS and DBIF datasets

Native Insect Species	Non-Native Plant Species	Number of Records in RHS	Number of Records in DBIF	Total Number of Records	Proportion of Records from RHS
Kakothrips pisivorus	Pisum sativum	102	1	103	0.99
Smynthurodes betae	Phaseolus coccineus	63	0	63	1
Delia antiqua	Allium cepa	60	1	61	0.98
Dasineura tetensi	Ribes nigrum	57	3	60	0.95
Phytonemus pallidus	Aster amellus	54	0	54	1
Unaspis euonymi	Euonymus japonicus	54	0	54	1
Delia platura	Phaseolus coccineus	43	0	43	1
Synanthedon tipuliformis	Ribes nigrum	41	1	42	0.98
Hyperomyzus lactucae	Ribes nigrum	30	1	31	0.97
Aphis (Bursaphis) schneideri	Ribes nigrum	28	2	30	0.93
Bryobia praetiosa	Ribes uva-crispa	23	0	23	1
Lichtensia viburni	Viburnum tinus	23	0	23	1
Thecabius (Parathecabius) auriculae	Primula auricula	19	1	20	0.95
Delia platura	Phaseolus vulgaris	19	0	19	1
Smynthurodes betae	Phaseolus vulgaris	18	0	18	1
Sitona (Sitona) lineatus	Vicia faba	13	3	16	0.81
Brachycaudus (Appelia) schwartzi	Prunus persica	14	0	14	1
Delia cardui	Dianthus caryophyllus	14	0	14	1
Aceria pseudoplatani	Acer pseudoplatanus	8	2	10	0.80
Cydia splendana	Castanea sativa	8	2	10	0.80
Saissetia coffeae	Nerium oleander	10	0	10	1
Delia platura	Vicia faba	6	2	8	0.75
Dysaphis (Pomaphis) pyri	Pyrus communis	7	1	8	0.88
Lampronia capitella	Ribes nigrum	7	1	8	0.88
Orthochaetes setiger	Cyclamen hederifolium	8	0	8	1
Aculops acericola	Acer pseudoplatanus	4	2	6	0.67
Delia cardui	Dianthus barbatus	5	1	6	0.83
Sitona (Sitona) lineatus	Pisum sativum	4	2	6	0.67
Trama troglodytes	Helianthus tuberosus	6	0	6	1
Delia antiqua	Allium porrum	4	1	5	0.80
Phytonemus pallidus	Aster novi-belgii	5	0	5	1

Uroleucon (Uromelan) jaceae	Centaurea cyanus	5	0	5	1
Colomerus vitis	Vitis vinifera	3	1	4	0.75
Unaspis euonymi	Euonymus fortunei	4	0	4	1
Craesus septentrionalis	Betula utilis	3	0	3	1
Dysaphis (Dysaphis) crataegi	Crataegus rhipidophylla	3	0	3	1
Elophila nymphaeata	Nymphaea nouchali	3	0	3	1
Eriophyes triradiatus	Salix fragilis	1	2	3	0.33
Helophorus (Empleurus) rufipes	Lactuca sativa	2	1	3	0.67
Lichtensia viburni	Hedera canariensis	3	0	3	1
Lichtensia viburni	Hedera colchica	3	0	3	1
Oligonychus ununguis	Picea abies	3	0	3	1
Oligonychus ununguis	Picea glauca	3	0	3	1
Pegomya setaria	Fallopia baldschuanica	1	2	3	0.33
Phytomyza rufipes	Brassica rapa	2	1	3	0.67
Pristiphora (Pristiphora) appendiculata	Ribes uva-crispa	1	2	3	0.33
Putoniella pruni	Prunus domestica	3	0	3	1
Synanthedon tipuliformis	Ribes uva-crispa	2	1	3	0.67
Aculus hippocastani	Aesculus hippocastanum	0	3	3	0
Aphthona euphorbiae	Linum usitatissimum	0	3	3	0
Atomaria (Atomaria) linearis	Spinacia oleracea	0	3	3	0
Cucullia absinthii	Artemisia absinthium	0	3	3	0
Cucullia absinthii	Artemisia vulgaris	0	3	3	0
Epinotia nanana	Picea abies	0	3	3	0
Epinotia nanana	Picea sitchensis	0	3	3	0
Eupithecia tantillaria	Picea abies	0	3	3	0
Eupteryx atropunctata	Solanum tuberosum	0	3	3	0
Haplodiplosis marginata	Triticum aestivum	0	3	3	0
Kalcapion semivittatum	Mercurialis annua	0	3	3	0
Longitarsus parvulus	Linum usitatissimum	0	3	3	0
Nematus (Kontuniemiana) olfaciens	Ribes nigrum	0	3	3	0
Phyllotreta nemorum	Sinapis arvensis	0	3	3	0
Phytomyza cytisi	Laburnum anagyroides	0	3	3	0
Phytomyza petoei	Mentha spicata	0	3	3	0
Rabdophaga triandraperda	Salix triandra	0	3	3	0
Sitodiplosis mosellana	Triticum aestivum	0	3	3	0
Therioaphis (Rhizoberlesia) riehmi	Melilotus officinalis	0	3	3	0

All insects above were uniquely associated with non-native plants in both the RHS and the DBIF. The above records represent the 67 most frequent associations between these native insects and non-native plants in the datasets. RHS insects were sampled in novel garden ecosystems, and DBIF insects were sampled in the wider landscape.

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